The relationships of the later Miocene Hominoidea

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ABSTRACT

Metrical methods for describing the variance in extant hominoids are applied to phenetic groupings of later Miocene hominoids in order to produce palaeospecies whose variance is compatible with that seen in living hominoids.

Enamel thickness measurements are presented for samples of living and fossil hominoids. An index of relative enamel thickness scaled for size has been developed and this defined four categories of relative enamel thickness metrically: Thin enamel (mean values of relative enamel thickness between 8.90 and 11.30), intermediate/thin enamel (mean values between 11.30 and 14.65), intermediate/thick enamel (mean values between 14.65 and 17.25), and thick enamel (mean values between 17.70 and 26.20). Thin enamel has been found in Pan, Gorilla and Hylobates; intermediate/thick enamel is found in Pongo; and thick enamel is found in Homo. Thick enamel is also found in Sivapithecus (17.73 - 21.69).

The distribution of enamel prism packing patterns at different depths in hominoid enamel show that Homo, Hylobates and Sivapithecus have almost entirely Pattern 3 enamel. Pongo has an outer thickness (less than 25%) of Pattern 1 enamel, and Pan and Gorilla have an outer (40%) thickness of Pattern 1 enamel overlying the Pattern 3 enamel. Pattern 3 enamel in hominoids is formed quickly (5 - 7 µm per day) and has well marked Hunter-Schreger bands. Pattern 1 enamel is formed slowly (less than 2 µm per day) and has no Hunter-Schreger bands.

On the basis of these new data the common ancestral condition of hominoid enamel has been shown to be thin enamel which formed at the fast (Pattern 3) rate. The common ancestor of the great ape and human clade had thick enamel which formed at the fast (Pattern 3) rate, and this was primitively retained in the common ancestor of the African ape and man clade and in the exclusively hominid clade. The common ancestor of the African apes had thin enamel, a large proportion of which (40%) formed at the slow (Pattern 1) rate. Thick Pattern 3 enamel evolved non-adaptively through the relative increase in dental developmental period, and dietary factors were only of subsequent importance in the maintenance of thick enamel.

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CHAPTER 1

INTRODUCTION

I. THE PROBLEM

The later Miocene hominoids present a heterogeneous sample whose relationships to one another and to living hominoids are presently unclear. Simons and Pilbeam (1965) recognised four groups of middle and upper Miocene hominoids to describe the morphological diversity of this sample. They recognised two sub-genera of Dryopithecus; D.(Dryopithecus) and D.(Sivapithecus), which were interpreted as primitive or "ape-like". Simons and Pilbeam (1965) suggested that Gigantopithecus represented a third morphological category which showed a variety of specializations but whose affinities were unclear. The fourth group of later Miocene hominoids was assigned to the genus Ramapithecus, which was considered to share specialised features with Australopithecus and Homo and was consequently interpreted to be the earliest known hominid (Simons and Pilbeam, 1965). The subgenus (Dryopithecus) was recognised for samples from Western Europe with one or two Asian representatives while (Sivapithecus) was recognised primarily for Asian specimens with the addition of a small sample of material from Eastern Europe. Gigantopithecus was only recognised in Asia, while Ramapithecus was recognised from Eurasia and Africa.

During the 1970s a substantial amount of new material was described from the later Miocene of Eurasia (de Bonis et al., 1974; Andrews and Tobien, 1977; Kretzoi, 1975; Pilbeam et al., 1977). This material was assigned to various of the categories defined by Simons and Pilbeam (1965) but led a number of workers to question the

distinctiveness of Ramapithecus from (Sivapithecus) and Gigantopithecus. Ramapithecus had previously been interpreted to represent the earliest known member of man's family, Hominidae. Many characters had been used to advocate this position but a number of these can be reduced to a suite of characters which appear to be interrelated to thick enamel, which became the principle component in discussions of the hominid affinities of Ramapithecus (e.g. Simons, 1976). New material of (Sivapithecus) and of Ramapithecus showed that these taxa were less distinct from one another than had previously been suggested. Sivapithecus was restored to full generic rank (Simons, 1976; Pilbeam, 1976; Andrews and Tekkaya, 1976). The similarity that was recognised between the dental morphology of Ramapithecus, Sivapithecus and Gigantopithecus was recognised to be the result of all of these taxa having molar teeth with thick enamel. Simons interpreted this similarity to be the result of parallel evolution (Simons, 1976) but others suggested that a close phylogenetic relationship between these three genera was indicated (Pilbeam et al., 1977; Pickford, 1977). Simons (1976) maintained the position that thick enamel, among other characters, in Ramapithecus indicated a close relationship to Australopithecus and Homo while others interpreted the similarity between Ramapithecus and Sivapithecus to mean that Ramapithecus was less hominid-like (Pilbeam et al., 1977; Andrews, 1977). In general it was considered that hominids were likely to have their origin in some part of the "thick-enamelled" hominoid group.

The morphological distinctiveness of the "thick-enamelled" hominoids

from Dryopithecus has been implicity questioned (Martin and Andrews, 1982; Kay, 1982b; Simons, 1976). Material from Rudabanya in Hungary was originally considered to represent Ramapithecus (Simons, 1976) but has subsequently been assigned to Dryopithecus (Martin and Andrews, 1982; Kay, 1982b).

Recently described cranial material of Sivapithecus has been interpreted as indicating a close phylogenetic relationship between Sivapithecus and Pongo (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Ward and Pilbeam, 1983). This has led to the re-examination of material assigned to Ramapithecus and some of these characters have been found to occur in that genus also (Lipson and Pilbeam, 1982). This has led a number of workers to suggest that thick enamel is not a uniquely human trait. A second school of opinion has interpreted the similarity between Ramapithecus and Sivapithecus to mean that the material assigned to these genera should all be interpreted as representing early members of man's family (Kay, 1982a, 1982b; Kay and Simons, 1983).

One of the crucial characters in these arguments has been enamel thickness and the way it has changed in hominoid evolution. Enamel thickness has not been defined in metrical terms and has not been documented at all in later Miocene hominoids with the exception of a single specimen of Ramapithecus (Gantt, 1977). Consequently the interpretations as to which fossil samples have thick enamel have been subjective, and the further interpretations of the phylogenetic significance of thick enamel have been speculative. There is, however, a degree of agreement between those who suggest that

Sivapithecus is related to the orang-utan and those who believe its affinities lie with early hominids. In both case thick enamel is considered to be an important taxonomic character and the "thin-enamelled" Dryopithecus has been largely ignored in recent works on the relationships of the later Miocene hominoids (Kay, 1982b; Kay and Simons, 1983; many contributions in Ciochon and Corruccini, 1983).

A major problem in the interpretation of the later Miocene hominoids is that little is known about the thickness of enamel even in extant hominoids. Consequently the significance of enamel thickness changes in hominoid evolution have been the subject of dispute. In the recent synthesis on hominoid evolution (Ciochon and Corruccini, 1983) enamel thickness was mentioned by the majority of contributors and alternative explanations of its evolutionary significance were abundant. Until enamel thickness has been defined in metrical terms and the polarity of enamel thickness changes in hominoid evolution has been established, the interpretation of the relationships of the later Miocene hominoids will continue to be assessed on the basis of each authors subjective interpretation of the significance of these characters. It is hoped that the resolution of these questions will clarify the relationships of the later Miocene hominoids. If enamel thickness can be fed into the equation of hominoid evolution based on empirical data then it is likely that more time will be devoted to examining other aspects of morphology which have tended to be ignored in the face of speculative assessments of the significance of enamel thickness.

II. THE AIMS OF THIS THESIS

1. The definition of palaeospecies units

One problem in the interpretation of the relationships of the later Miocene hominoids has been the definition of species units of fossil specimens. In a number of cases later Miocene hominoids from a particular site present a morphologically homogeneous sample which has been suggested to be too variable to be considered to represent a single species. In this work I shall attempt to develop a framework for the grouping of fossil specimens into morphologically homogeneous units. The aim will be to avoid overemphasis on the more complete specimens in a fossil sample as this tends to assume that such specimens are centrally placed in the range of variation of the species to which they belong, which is unlikely to be valid.

Following the definition of a morphologically homogeneous fossil sample it is necessary to determine whether the variance in the sample is compatible with the variance seen in modern hominoids, if palaeospecies are to approximate biospecies. The metrical definition of variance in modern samples of hominoids will be analysed in an attempt to develop methods for quantifying variance in fossil samples. In particular I shall attempt to develop variance analysis methods which may be applied to fossil samples of small size and unknown sexual composition.

2. The measurement of enamel thickness

One of the major aims of this thesis is the assessment of the usefulness of enamel thickness for determining the relationships of the later Miocene hominoids. The first stage in achieving this aim will be to document enamel thickness in modern, as well as fossil, hominoids. Serial sections of human molars will be prepared so as to determine the influence of the plane of section on enamel thickness measurement. It is hoped that this will permit the development of a method which minimises tissue destruction and minimises the influence of obliquity of section on the enamel thickness measurements. Having developed a method which complies with these requirements, a much larger sample of teeth of extant great apes and of archaeological *Homo sapiens* than has previously been available will be sectioned for enamel thickness measurement. In addition, teeth from four species of later Miocene hominoid will be sectioned for enamel thickness measurement.

A number of different measurements of enamel thickness will be taken and each of these will be assessed for its ability to summarise and characterise the distribution of enamel over the tooth crown. The measurement which best achieves this aim will then be used as the primary figure by which to express enamel thickness. The directly measured enamel thickness data will be compared to estimates of enamel thickness arrived at by non-destructive methods (Simons, 1976; Kay, 1981). If these methods are found to provide accurate measurements of enamel thickness then they will be employed to provide enamel

thickness data for a taxonomically broader sample of primates.

Tooth size measurements which exclude any contribution from the enamel will be used to examine the possible influence of tooth size (body size) on within species variations in enamel thickness. It has been suggested that larger anthropoid species tend to have thicker enamel than do smaller anthropoids (Kay, 1981; Gantt, 1977). A number of dental estimators of body size will therefore be used for scaling enamel thickness measurements in order to permit the comparison of enamel thickness among species of different size. An attempt will be made to devise a single number measurement of enamel thickness which takes account of the size of the animal. The successful achievement of this aim would greatly facilitate comparisons of enamel thickness among species of differing size. If a size independent measurement of enamel thickness can be developed then this will be used to define size independent categories of enamel thickness on the basis of metrical data. Finally, an attempt will be made to determine the morphocline polarity, and the evolutionary significance, of enamel thickness changes in hominoid evolution.

3. The taxonmic value of enamel microstructure

It has been suggested that hominids have a different kind of enamel prism packing pattern than do the great apes (Gantt, et al., 1977). If this is the case then the documentation of the enamel microstructure in later Miocene hominoids may considerably assist attempts to determine their relationship to modern species and will be

particulary important in the assessment of Ramapithecus.

Some of the specimens which will be used for enamel thickness measurements will therefore be used to determine the enamel prism packing pattern in great apes and humans as well as in species of later Miocene hominoid. If taxonomically useful data can be obtained then this will be used for the determination of the relationships of those species of later Miocene hominoid which are available for this study.

In addition, the longitudinal sections cut for enamel thickness measurements will be examined in order to see whether they can be used to provide evidence as to how the observed thickness of enamel has been developed. It has been suggested that incremental features observed in polished longitudinal thin sections observed by light microscopy represent fixed periods of enamel secretion (Boyde, 1964). An attempt will therefore be made to observe these features (prism cross striations, incremental lines) on the face revealed by the cut for enamel thickness measurements. Light microscopic methods cannot be used unless polished thin sections are prepared and this will not be possible in the present work as the conservation of tissue is of paramount importance. Instead, scanning electron microscopy will be used to determine whether incremental features are preserved in fossilised specimens.

The aim is therefore to establish whether taxonomically significant differences in enamel prism packing patterns exist within the

Hominoidea. Secondly, to attempt to obtain evidence as to how the observed enamel thickness has developed. If there are distinctions in enamel microstructure among hominoids an attempt will be made to determine the functional consequences of these for the species in which they are found.

4. The polarity of enamel thickness changes in hominoid evolution

An attempt will be made to explain the distribution of enamel thickness among hominoids and to determine the condition of enamel thickness in the various hominoid clades. As well as enamel thickness data, microstructural data relating to the cell biological processes by which the thickness has been developed will be employed. It is hoped that the combination of these data will permit a definite assessment of the condition of enamel thickness in the common ancestors of the various hominoid clades. If this is not possible then the alternative explanations will be assessed as to which would be the most parsimonious. If this results in a number of equally likely alternatives these will be reported and the significance of each of them discussed.

5. The relationships of the later Miocene Hominoidea

The relationships of the later Miocene hominoids will be determined on the basis of the morphology of the palaeospecies units defined in this work. The polarity of each character which diagnoses a species or genus will be assessed. Where possible, fossil genera will be attributed to a particular position in hominoid phylogeny on the basis

of shared dervied characters. When a number of possible interpretations are equally likely these will each be discussed and the most likely selected. Alternatively, it may not be possible to select one interpretation in which case the possible relationships of a fossil taxon will be listed but the taxon will not be assigned to any particular position in hominoid phylogeny.

III. METHODS (SYSTEMATIC FRAMEWORK)

The majority of methods employed in this study are particularly applicable to one area of the study, and so the methods are described in detail in each Chapter. The exception to this is the overall systematic framework of this thesis which is applicable to the thesis as a whole and is described below.

The assessment of the relationships of hominoid species to one another is based on the methods described by Hennig (1966). This method, which has become known as cladistics or phylogenetic systematics, was not a new development by Hennig. He formalised and rigourised the definition of the characters which are the most useful for the determination of relationships between taxa. In this method the only characters which have any significance for the determination of a relationship between taxa are shared dervied characters (synapomorphies). The possession of a primitive character which has been retained from the common ancestor of the taxa in question is of no value for determining their relationships, and these characters are termed symplesiomorphic. The principles and methods of phylogenetic

systematics have been refined from the work of Hennig (1966) and particularly clear descriptions of the method may be found in Delson et al., (1977; Delson, 1976) and Olson (1978).

One of the major problems in cladistics is that the determination of whether a character is derived or primitive is somewhat subjective. It is particularly important to note that characters are derived or primitive with reference to particular nodes or branching points in a cladogram. A derived character which defines the great ape and human clade is derived with respect to the common ancestor of the Hominoidea but within the great ape and human clade it is a primitive retention from the common ancestor of the great ape and human clade. Its presence in only some members of that clade is not evidence that they are particularly closely related. In the present work the polarity of a character with respect to a particlar branching point has been assessed on the basis of parsimony. In other words, the interpretation of the ancestral condition is adopted which requires the least number of modifications to explain the distribution of the character in members of the clade. The only exceptions to this were made when another source of evidence, such as developmental data, was available.

A major criticism of the cladistic approach has been that, if rigorously applied, the method of producing a classification of the species involved results in a highly unstable nomenclature. This aspect of cladistics can be completely separated from the determination of relationships, however, and a more traditional and

subjective approach to the classification of species can be adopted. In the present work I have followed cladistic principles in that I was not prepared to recognise taxonomic categories for groups which were not monophyletic (e.g. Pongidae, for the great apes). However, I have not felt that it was necessary to recognise each proposed branching point in a cladogram nomenclatorially. I have found it more appropriate to present cladograms to illustrate relationships rather than to devise new classifications.

IV. MATERIAL INCLUDED IN THIS STUDY

The fossil material which I have included in this study is listed in detail in Chapter 3. It includes all of the material whose descriptions are mentioned in the literature review in Chapter 3. This means that I have studied all of the later Miocene material, in the original, with a few important exceptions. The material which I have only studied from casts is as follows:

Specimens from Moroto, Uganda.
Gigantopithecus blacki, mandibles from China.
Isolated teeth from the Miocene of Germany.
The holotype of simonsi (Kay, 1982b) which has been lost.
Holotypes of R.lufengensis and S.yunnanensis.
Hominoid mandible from Indo-Pakistan in the collection at Chandigarh.
MTA-2125, and A.meteai type mandible.

The later Miocene material which I have not examined in cast or original is as follows:

No material from China has been studied with the exception of the five mandibles listed above.

Material in the collection of the Senckenburg Museum.

Material in the collection at Chandigarh.

Type mandible of S.alpani.

With these few exceptions I have been able to examine all described, as well as a large amount of undescribed, material of later Miocene hominoids from Eurasia and Africa.

The specimens used for enamel thickness and enamel microstructure research are listed in detail in Chapters 4 and 5 and in Appendix A.

Comparative observations of modern hominoids have been made on specimens in the collection of the British Museum (Natural History).

V. DEFINITIONS

1. Museum accession prefixes used in this thesis:

AMNH	American Museum of Natural History
BMdHN	Bordeaux Museum d'Histoire Naturelle, France
BP	Bursa-Pasalar specimens currently housed at the BM(NH)
BSPhG	Bayerische Staatssammlung fur Palaontologie and Historische Geologie in Munich, West Germany
CYP	Chandigarph/Yale Project, housed at Chandigarh, India
Erlangen	Un-numbered specimen at the Geologisches Institut Erlangen, Germany, currently on loan to the author at the BM(NH)
GSI D	Geological Survey of India, Calcutta
GSP	Geological Survey of Pakistan, currently housed at Peabody Museum, Harvard University, U.S.A.
GSP-S	Geological Survey of Pakistan, Sind collection, currently housed at the Peabody Museum, Harvard University, U.S.A.
IPS	Instituto Provincial de Paleontologia, Sabadell, Spain
Klagenfurt	Un-numbered specimen at the Karntner Landesmuseum, Klagenfurt, Austria
KNM FT	Kenya National Museum, Fort Ternan collection
KNM MB	Kenya National Museum, Maboko Island collection
KNM MJ	Kenya National Museum, Majiwa and Kaloma collection
M	British Museum (Natural History)
MNHNP	Museum National d'Histoire Naturelle, Paris, France
MTA	Maden Tetkik ve Arama Enstitusin, Ankara, Turkey

NHMW	Naturhistorisches Museum Wien, Vienna, Austria
ONGC.V	Oil and Natural Gas Commission, Dehra Dun, India
PUA	Punjab University, Anthropology, Chandigarh, India
RPL	Rain Ravine, Macedonia, Greece. One specimen housed at University of Thessaloniki, Greece, bulk of collection currently housed at University de Poitiers, France
Rud	Rudabanya, Hungary. Specimens in the care of Prof. M. Kretzoi
Seo de Urgel	Un-numbered specimen housed at the Seminario Conciliar of Barcelona, Spain
YPM	Yale Peabody Museum, U.S.A.

2. Measurements, techniques and abbreviations

Measurements were taken with a dial caliper and were recorded to the nearest 0.1 mm. The measurements employed in this thesis were the mesial to distal length and the buccal to lingual breadth of the crowns of all teeth except for canines and first lower premolars. These measurements are abbreviated as M-D and B-L. For the canines and the lower first premolar (P_3) the maximum length along the long axis of the tooth, and the minimum breadth of the crown measured perpendicular to the axis of maximum length were taken. These measurements are listed as C^1 Max. and P_3 Perp. etc. For the molar teeth the mesial to distal length of the cervix, and the buccal to lingual breadth of the cervix across the mesial cusps were also used. These are abbreviated as M-DR and B-LR. Where these measurements were used in conjunction with crown length and breadth,

the crown dimensions are listed as M-DC and B-LC respectively. The measurements were taken in the same way as those reported by Pilbeam (1969) and Andrews (1978) and more detailed definitions can be found in those references.

Two dimensions of the mandibular corpus have been used in the present work. These are the corpus vertical depth and the corpus perpandicular breadth, or thickness, at the position of the lower first molar.

The detailed measurements of enamel thickness are listed and defined in Chapter 4.

3. Univariate statistics

The following univariate statistics have been used, and abbreviated as follows. Definitions and formula are not given here unless they differ from those of Simpson et al., (1960).

n = sample size

Mean = arithmetic mean value for the sample

Min = the minimum value encountered in the sample

Max = the maximum value encountered in the sample

Range = the difference between the minimum and the maximum value encountered in a sample

Range mid-point = the average of the minimum and the maximum values

Variance = variance

C.V. = coefficient of variation

S.Deviation = Standard deviation

V_{cor} = C.V. corrected for small sample size (Pilbeam, 1969 p.10)

S.E. = Standard error

$\frac{(S.E. \times 100)}{mean}$ = Standard error expressed as a percentage of the mean. This is used as a guide to the adequacy of the sample size (Pilbeam, 1969 p.9)

Sample low 95% = the lower 95% confidence limit for the sample

Sample high 95% = the upper 95% confidence limit of the sample

Mean low 95% = the lower 95% confidence limit of the mean

Mean high 95% = the upper 96% confidence limit of the mean

4. Bivariate statistics

Linear regression has been used in all cases.

r = correlation coefficient

r^2 = the proportion of the variance explained by the regression, expressed as a percentage

sig level = significance level of the correlation

y/x = intercept on the y-axis

slope = computed slope of the line

S.x = standard deviation of the x-variable

S.y = standard deviation of the y-variable

S.yx = the standard deviation of regression. This reduces the variation of the y-variable by the amount of this variance which is explained by the regression (Hills, personal communication). $S.yx \simeq \sqrt{(1 - r^2)}\ (S.y)$

5. Indices

The following indices have been used, they are explained fully in Chapter 2.

Range/mean = the range expressed as a percentage of the arithmetic mean for a variable.

Sexual dimorphism index = the male mean/the female mean for a variable

Sexual overlap index = the male minimum/the female maximum

Maximum variation index = the maximum (male) value/the minimum (female) value

Specimen sex index = C1 maximum length/M1 M-D length

Relative incisor size = I^1 M-D/I^2 M-D

Relative central incisor size = I^1 M-D/M^1 M-D

Relative premolar size = P^3 M-D/M^1 M-D; P^4 M-D/M^1 M-D; P^4 M-D/M_1 M-D.

CHAPTER 2

THE DESCRIPTION OF VARIANCE IN EXTANT HOMINOIDEA

I. INTRODUCTION

1. Introduction

The way in which fossil specimens are grouped into taxonomic units, palaeospecies, depends on the combination of phenetically compatible groups of specimens. Although it was recognised that a fossil species is not homologous with a modern species it has been my aim to define palaeospecies so that they are compatible with the morphological and metrical variation encountered in biologically defined extant hominoid taxa. Morphological variation was considered subjectively on the basis of a knowledge of extensive samples of modern species and of the fossil specimens. Metrical data were assessed for their utility in defining a palaeospecies unit which has similar degrees of variance to that encountered in modern species. Particularly important in this regard are statistical descriptions of variation and of sexual dimorphism. A number of approaches to this problem have recently been suggested (Gingerich and Schoeninger, 1979; Martin, 1981; Kay, 1982a, b). These methods must be examined rigorously before they may be used with confidence. Particular care must be taken to avoid the confusion which may arise due to the comparison of biased samples and/or samples of different numbers of specimens. A number of these methods were combined for defining taxa within morphologically homogeneous and metrically continuous samples of fossils, and these methods, described below, were applied to the later Miocene hominoid sample in Chapter 3.

2. Living hominiod phylogeny

a. Molecular evidence

Traditionally the Hominoidea have been divided into three families: the Hylobatidae, the Pongidae, and the Hominidae. These have been defined to contain Hylobates (and Symphalangus, when this genus has been considered distinct), Pan, Gorilla and Pongo (the three genera of great apes), and Homo respectively (Napier and Napier, 1967; Simpson, 1945). Szalay and Delson (1979) maintained these groupings as subfamilies within the family Hominidae. The relationships of the living hominoid primates have been clarified by the biomolecular work initiated some twenty years ago by Morris Goodman. The interpretation of evolutionary trends through protein similarities and differences in living animals has fallen into two major areas; firstly the recognition of cladogenic events, or evolutionary branching sequences, and secondly the so-called "molecular clock".

The molecular clock is still the subject of considerable controversy (see the many contributions in Ciochon and Corruccini, 1983). In my opinion the molecular clock is of some interest as far as biogeography and the assessment of fossil deposits of potential interest are concerned, though its limitations must be recognised even here, but it has no place in the taxonomic assessment of fossil species. In other words I would not be prepared to accept that a fossil older than a particular age is restricted as to which taxa it could belong to on the basis of interpretations of the molecular data regarding the dates of particular cladogenic events. I prefer the approach taken by

Andrews and Cronin (1982; Andrews, 1982) in assessing the fossil evidence on the basis of morphology and then comparing these interpretations with the "molecular clock" data. When the two sources of data are compatible this is of interest, but when they are not this requires both lines of evidence to be reexamined. I see no good reason to favour one line of evidence in preference to the other on purely *a priori* grounds. As such the "molecular clock" is of only peripheral interest as far as the present work is concerned.

Two cladogenic events in hominoid evolution are well documented through the analysis of blood groups and histocompatibility antigens, chromosome banding patterns, protein structure and antigenicity, amino acid sequences of proteins, and DNA endonuclease restriction mapping, sequencing and reassociation kinetics (King and Wilson, 1975; Bruce and Ayala, 1979; Socha and Moor-Jankowski, 1979; Ferris et al, 1981; Stanyon and Chiarelli, 1982; Yunis and Prakash, 1982; Cronin, 1983; Goodman et al, 1983; Zihlman and Lowenstein, 1983). These are the initial divergence of the *Hylobates* clade from the clade comprising the great apes and man; and the subsequent divergence of the orang-utan from the African apes and man clade (Figure 2.1). The other three cladogenic events necessitated by the separation of the two species of *Pan*, one species of *Gorilla* and one species of *Homo*), are the subject of some dispute.

These views on the separate divergence of the gibbon and the orang-utan clades from the rest of the hominoids have a major implication for hominoid taxonomy. A family group for the four living

great apes recognises similarity in grade, mainly from shared primitive characters, but is not justified if phylogenetic considerations are paramount. This grade is described by the vernacular term "great apes", and there seems no good reason to maintain a family for them as this contradicts the evidence regarding phylogeny.

There is less consensus regarding a third cladogenic event; the divergence of the African ape and human stock. Many authors support a three way split of Pan, Gorilla and Homo. Others have argued in favour of Pan and Homo having shared a common ancestor to the exclusion of Gorilla; to Gorilla and Homo having shared a common ancestor to the exclusion of Pan; and to Pan and Gorilla having shared a common ancestor to the exclusion of Homo. Biochemically chimpanzees and bonobos show closer affinities to one another than to either gorillas or humans, even though Pan paniscus and P.troglodytes are separable electrophoretically (Goodman et al, 1970; Cronin, 1977) and Karyologically (Khudr et al, 1973).

Before 1970 chromosomes were examined solely on the basis of number and gross morphology. These data supported the great similarity of Pan, Gorilla and Homo and the distinctiveness of Pongo (Chiarelli, 1962; Chu and Bender, 1962; Hamerton et al, 1963). Miller (1977) and Seuanez (1979) point to evidence that Homo is more closely related to Gorilla than either are to any other living species.
A cladistic approach by Stanyon and Chiarelli (1982) does not support this latter interpretation but suggests that derived karyological

features indicate that Gorilla and Pan shared a period of common ancestry after the divergence of man. This position is adopted in Figure 2.1.

b. Morphological evidence

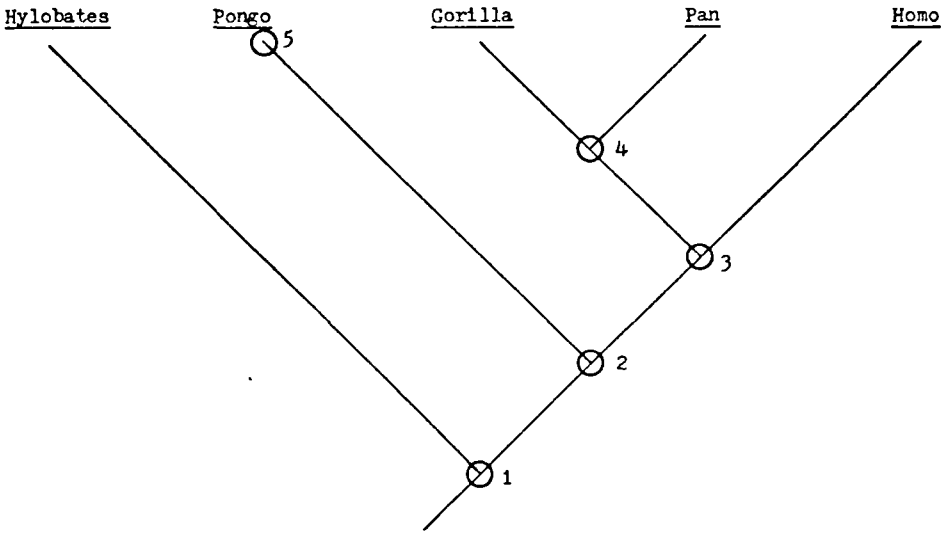
In spite of the growing evidence from molecular and karyological studies, morphologists were slow in accepting that the great apes could no longer justifiably be grouped as a family. A number of workers have confirmed the morphological distinctiveness of Pongo (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Kay, 1982b; Ward and Pilbeam, 1983; Kay and Simons, 1983). However, this distinctiveness does not, in itself, confirm that Pongo is the sister group of the african apes and man. These characters could be autapomorphic in Pongo and little morphological evidence can be cited to support a close relationship between the African apes and man, which excludes Pongo, other than shared primitive characters. The morphological characters defining hominoid clades are listed in Figure 2.1.

However, during the last five years the biomolecular and the morphological evidence (see notes for Figure 2.1) have been combined to produce a consensus regarding the relationships of the extant hominoids: Pan troglodytes and Pan paniscus are sister species; Pan and Gorilla form a sister group; African apes are the sister group of Homo; the African apes and man are the sister group of Pongo; the great apes and man are the sister group of Hylobates (Figure 2.1). In

the most recent synthesis on hominoid evolution (Ciochon and Corruccini, 1983) this interpretation was supported by the overwhelming majority of contributors. It is noted that the biomolecular evidence does not unanimously support the linking of Pan and Gorilla to the exclusion of Homo but few workers would suggest that biomolecular data refuted such a hypothesis, rather that they were unable to support any particular interpretation as to the branching pattern within the African ape and human clade. There is some karyological evidence (Stanyon and Chiarelli, 1982) which suggests that Pan and Gorilla shared a period of common ancestry after the divergence of man. The shared derived postcranial specializations associated with knuckle walking support this interpretation (see notes for Figure 2.1).

The relationships shown in Figure 2.1 will be used as the current best hypothesis regarding the relationships of the extant hominoids as it is consistent with both biomolecular and morphological evidence. Apart from this general discussion the characters which define this cladogram will not be further discussed at present. The characters which have previously been used are reappraised and combined with new data regarding enamel thickness and enamel microstructure in Chapter 6. For the present it is only necessary to remark that there are no significant disagreements regarding the constitution of species within the Hominoidea and particularly within the great ape and human clade. The aim of this chapter was therefore to devise ways to describe the variance in extant hominoid species in a way which may be used to combine or divide morphologically homogeneous fossil samples.

Figure 2.1: Morphological evidence for the relationships of the extant Hominoidea.



Derived characters defining branching points:

Node 1:

Pattern 3 enamel prism packing (Boyde and Martin, 1982, 1983).

Palate relatively broad anteriorly (Harrison, 1982).

Upper I^1 low crowned and broad (Harrison, 1982).

I^2 modified from narrow conical shape (Delson and Andrews, 1975).

Incisors large relative to molars (Harrison, 1982).

P_3 with only moderate sized honing face (Harrison, 1982).

Trigon cusps quite rounded (Harrison, 1982).

Reduced cingulum on cheek teeth (Harrison, 1982).

Increased length of the cervical vertebral region (Schultz, 1938, 1961).

Increased diameter and reduced length of the vertebral centra (Ankel, 1972; Rose, 1975).

Shortening of lumbar region of vertebral column to a mode of five (Schultz, 1961).

No external tail. Reduction not by atrophy but by transformation into the shelflike coccyx (Andrews and Groves, 1976).

Scapula dorsally positioned with glenoid fossa directed more cranio-laterally (Le Gros Clark, 1959; Washburn, 1963; Oxnard, 1967; Corruccini, 1975).

Large acromian and coracoid processes on the scapula (Corruccini, 1975).

Sternum short and broad with a reduced number of sternal elements (Schultz, 1930, 1961).

Humerus head large, symmetrical and rounded (Oxnard, 1963; Andrews and Groves, 1976).

Olecranon fossa relatively deep and well defined (Harrison, 1982).

Distal humerus with broad trochlea relative to capitulum with midportion constricted (Morbeck, 1983).

Lateral edge of trochlea that separates trochlea and capitulum anteriorly wraps around distally to meet with olecranon fossa (Morbeck, 1983).

Ulnar olecranon process reduced (Tuttle, 1975).

Development of an intra-articular meniscus which partially isolates the styloid process from direct contact with the triquetrum and pisiform (Lewis, 1969).

Extensive distal radio-ulna articulation (Harrison, 1982).

Proximal ulna with segmented trochlear notch and U-shaped deep radial notch (Morbeck, 1983).

Radial head approaches circularity and is not tilted (Harrison, 1982; Rose, 1983).

Styloid process of radius greatly reduced (Harrison, 1982).

Femur neck lacks tubercle (Harrison, 1982).

Femur with deep and restricted trochanteric fossa (Harrison, 1982).

Calcaneus relatively short and broad (Harrison, 1982).

Development of vermiform appendix (Le Gros Clark, 1959; Groves, 1972; Andrews and Cronin, 1982).

Development of pelvic diaphragm (Tuttle, 1975).

Node 2:

Palate long and deep anteriorly (McHenry et al., 1980).

I^2 broad (Harrison, 1982).

P_3 broadened, reduced canine honing (Delson and Andrews, 1975).

M_3 shortened and broadened with large hypoconulid (Delson and Andrews, 1975).

Premolars lengthened with respect to molars (Delson et al., 1977).

Canines robust (Andrews and Cronin, 1982).

Inferior margin of orbits does not overlap the superior portion of the nasal aperture (Harrison, 1982).

Inferior transverse torus well developed and dominant over superior torus (Harrison, 1982).

Nasal bones relatively long (Harrison, 1982).

Humerus with well developed trochlear keel (Harrison, 1982).

Breadth of trochlear equal to or exceeding that of the capitulum (Harrison, 1982).

Cartilaginous meniscus fully interposed between greatly reduced ulnar styloid process and pisiform, resulting in total exclusion of ulnar-carpal articulations (Lewis, 1969, 1972).

Ontogenetically late appearance of ischial callosities (Delson and Andrews, 1975).

Pectoralis abdominis absent (Andrews and Groves, 1976).

Node 3:

Development of supra-orbital brow ridges. Expansion of glabella.

Presence of fronto-ethmoidal sinus (Delson and Andrews, 1975; Cave and Haines, 1940).

Incisive fossa divided into two chambers by the vomero-nasal contact,with the hard palate being deflected beneath nasospinale resulting in the formation of a true incisive canal (Ward and Pilbeam, 1983).

Large sphenopalatine fossae (Andrews and Cronin, 1982).

Node 4:

Prominant bony ridge on dorsodistal aspect of radial articular surface and on distal surface of scaphoid (Tuttle, 1975).

Volar and ulnar inclination of concave articular surface of the distal radius (Tuttle, 1974, 1975).

Prominent transverse ridge at base of dorsal articular surface of metacarpal heads (Tuttle, 1967, 1969).

Pronounced extension of the articular surface onto the dorsal aspect of metacarpal heads II-V (Tuttle, 196?

Presence of knuckle pads over the dorsal aspects of the middle phalanges (Schultz, 1936; Tuttle, 1969).

Extremely strong development of the flexor digitorum superficialis (Tuttle, 1975).

Deep and extremely well defined olecranon fossa (McHenry, 1975; Tuttle, 1975).

Node 5:

Palate not deflected beneath premaxilla (Ward et al., 1983).

Strong wrinkling of molar enamel (Delson et al., 1977).

I^1 much larger than I^2 (Andrews and Tekkaya, 1980).

Interorbital distance greatly reduced (Andrews and Cronin, 1982; Delson et al., 1977).

Orbits higher than broad (Andrews and Cronin, 1982).

Nasal bones relatively narrow (Delson et al., 1977).

Nasal cavity floor smooth and unstepped (Andrews and Cronin, 1982).

Deep and widely flaring zygomatic processes (Andrews and Tekkaya, 1980).

Zygomatic foramina above the level of the lower rim of the orbit, large and multiple (Andrews and Cronin, 1982).

Presence of a pronounced malar notch on the inferolateral aspect of the zygomatic (Preuss, 1982).

Restricted incisive foramen (Andrews and Cronin, 1982).

Incisive canal very narrow (Ward et al., 1983).

Palatine foramen very narrow and slit like (Andrews and Cronin, 1982).

Hallux reduced dramatically, often resulting in absence of distal phalanx (Tuttle and Rogers, 1966).

Metatarsal and proximal and middle phalangeal bones of digits II-V possess marked degree of curvature important in powerful grasping (Tuttle, 1970).

II. THE DESCRIPTION OF VARIANCE IN EXTANT HOMINOIDEA

1. Introduction

A number of sites at which later Miocene hominoids are represented present morphologically homogeneous samples which cover a wider range of size than is usually encountered in living primates (e.g. Pasalar, Siwaliks, Can Ponsic, Can Llobateres etc.). The way in which these samples are divided into species categories depends on the interpretation of the variance of the sample. Ideally the sample would be divided into males and females so that the number of size categories of each sex could be determined. In practice this is difficult even for the most complete specimens but it is a useful approach when complete specimens are available. Metrical methods for the recognition of sex in fossil specimens are considered below. A number of statistical analyses of variance have been used to define palaeospecies and these are considered with reference to data from extant hominoids.

2. Coefficient of Variation (C.V.)

The coefficient of variation for a dimension may be used as a size independant expression of variance (Gingerich and Schoeninger, 1979). Kay (1982b) has applied this method to later Miocene hominoid samples. However, this method has the disadvantage that it is very much sample size dependant. The only way that the method applied by Kay (1982b) can be used reliably is if the modern samples are constituted in exactly the same way as the fossil sample whose

variance is being analysed. Kay (1982b) calculated the coefficient of variation for dental dimensions for balanced mixed sex samples of modern species. This necessarily means that an equal number of male and female examples of the tooth must be present in the fossil sample if the data are to be directly comparable, because unequal sexual composition may result in increased coefficients of variation (Kay, 1982b). Despite these drawbacks, Kay (1982b) has also suggested that coefficients of variation measure the sexual dimorphism of the sample.

The samples of modern hominoids used in the analyses in this chapter are shown in Table 2.1. Since dental specimens, often isolated teeth, form the largest part of the later Miocene sample dental measurements have been used in the analysis. Coefficients of variation were calculated for males and females separately as well as for mixed sex (but not sex balanced) samples of modern hominoids (Table 2.2). Kay's (1982b) assumption is that coefficients of variation will be at a maximum in mixed sex samples. This was not found to be the case in quite a large number of cases even for the large sample sizes derived from Pilbeam (1969). For this reason each species has a maximum CV column in Table 2.2 which indicates when the CV in one sex exceeds that in the mixed sex sample. The reasons why this should be the case are not immediately clear. It could result from the different sample sizes in the single sex sample and the mixed sex sample. This could be tested by calculating CVs for equal sized samples of each sex for the mixed sex sample. If sample size were the reason for this discrepancy then it would mean that comparative data would need to be calculated to match each fossil sample separately in order that fossil

species could be defined to match the variance in a modern sample of the same size. If a fossil sample of 20 teeth is being analysed then CVs for 20 males, 20 females, and 20 exactly matched mixed sex teeth should be calculated.

In the present work the maximum observed CV has been used regardless of whether it results from a single or a mixed sex sample. The maximum value encountered among Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygameus and Hylobates lar is shown in Table 2.3. Also shown are the maximum values which Kay (1982b) reported for mixed sex samples. These two sets of data were combined to produce a range of CV values which define the maximum variance found in living hominoids. The least variable teeth in hominoids are the breadth of M^1 and the length of M_1 for upper and lower teeth respectively. When a fossil sample has a CV which exceeds these values (6.4 for upper M^1 breadth, and 6.2 for lower M_1 length) then the sample should be further examined to determine whether this high CV results from sample size or composition or from the combination of more than one species. Methods for this are discussed below.

When a fossil sample has a CV beyond the range for extant hominoids then more than one species may be being sampled. However, it should be borne in mind that a fossil sample with a CV within the hominoid range does not necessarily mean that only one species is being sampled. For example, if the buccal to lingual breadth measurements for M^1 in mixed sex samples of Hylobates hoolock and H.syndactylus (n = 11 and n = 12 respectively) are combined these result in a CV of

4.23 which is less than the CV for the same measurement in 14 male H.lar. (Table 2.2). I would expect the same situation to arise if measurements of Bonobo and Chimpanzee were combined, although because individual data points for Pan paniscus have not been published I have been unable to confirm this. Similarly if M^1 breadths for Pongo (n = 22) and Gorilla (n = 40) are combined they produce a CV of 9.4 which is only slightly greater than the value reported by Kay (1982b) for Siwalik M^1s.

It should particularly be noted that sample size will be influencing these values. If a fossil sample of 20 specimens has a CV exceeding that for a sample of the same size and composition for living hominoids then it might be assumed that two species are present. However, to test this requires the use of samples of 10 specimens from 2 modern species. Such a procedure is complicated, especially if a number of randomly selected samples are used for the comparative data, and I believe the impression is sometimes given of an objectivity and reliability which is not justified. For example, I have shown that two species of similar sized hylobatids have a CV well within the "single species" range defined by Kay (1982b). What this means is that CV can only be used to say that there is probably more than one species present. It cannot be used to confirm that a single species is present or to determine the number of species present. If a CV below the limit in living hominoids is found then I would contend that no evidence is present regarding the number of species present. If a CV of more than the maximum value is found then it is likely that more than one species is present. In other words the limits of

resolution of the CV method are such that it has limited value.

Kay and Simons (1983; Kay, 1982a, 1982b) have argued that a high CV means high sexual dimorphism and a low CV means low dimorphism. This does not conform with the data (Table 2.2). In many cases the CV in one sex is greater than that in the mixed sex sample and in most cases the CV in each sex is nearly as large as that for the mixed sex sample. Any difference in CV between the single sexed sample and the mixed sex sample may measure sexual dimorphism but it is by no means the major component of the CV value in a mixed sex sample. Unless these problems of high CVs in single sex samples compared with the value in mixed sex samples can be resolved by matching sample sizes using random selections from the single sex samples to produce the mixed sex sample then CV has little to contribute to the precise quantification of sexual dimorphism and interpretations based on this should be treated with caution.

Table 2 1: Sample sizes of extant hominoids used for the analyses in this chapter, by sex and tooth measurement.

	P.troglodytes			P.paniscus			G.gorilla			P.pygmaeus			H.syndactylus			H.lar		
	m	f	m+f	m	f	m+f	m	f	m+f	m	f	m+f	m	f	m+f	m	f	m+f
I^1 M-D	0	0	0	15	20	41	0	0	0	12	9	21	6	5	11	14	7	21
I^1 B-L	0	0	0	15	21	42	0	0	0	12	9	21	6	5	11	14	7	21
I^2 M-D	0	0	0	13	20	38	0	0	0	11	10	21	6	5	11	14	7	21
I^2 B-L	0	0	0	13	20	38	0	0	0	12	10	22	6	5	11	14	7	21
C^1 Max	14	12	26	15	18	33	20	20	40	12	9	21	7	5	12	13	7	20
C^1 Perp	14	11	25	15	18	33	20	20	40	12	9	21	7	5	12	13	7	20
P^3 M-D	14	12	26	17	26	50	20	20	40	12	10	22	7	5	12	14	9	23
P^3 B-L	13	11	24	17	27	51	20	20	40	12	10	22	7	5	12	14	9	23
P^4 M-D	14	12	26	16	23	45	20	20	40	12	10	22	6	5	11	14	9	23
P^4 B-L	13	11	24	16	24	46	20	19	39	12	10	22	6	5	11	14	9	23
M^1 M-D	14	12	26	32	41	93	20	20	40	12	10	22	7	5	12	14	9	23
M^1 B-L	12	11	23	32	41	93	20	20	40	12	10	22	7	5	12	14	9	23
M^2 M-D	14	12	26	18	27	52	20	20	40	12	10	22	7	5	12	14	9	23
M^2 B-L	13	11	24	18	27	52	20	20	40	12	10	22	7	5	12	14	9	23
M^3 M-D	11	10	21	11	11	24	20	20	40	12	10	22	7	5	12	13	9	22
M^3 B-L	11	9	20	11	11	24	20	20	40	12	10	22	7	5	12	13	9	22
I_1 M-D	0	0	0	16	22	43	0	0	0	11	9	20	7	3	10	14	9	23
I_1 B-L	0	0	0	15	22	43	0	0	0	11	9	20	7	3	10	14	9	23
I_2 M-D	0	0	0	17	24	47	0	0	0	11	9	20	7	3	10	13	9	22
I_2 B-L	0	0	0	17	24	47	0	0	0	11	9	20	7	3	10	13	9	22
C_1 Max	13	11	24	16	20	37	20	18	38	12	9	21	7	4	11	14	8	22
C_1 Perp	14	11	25	16	20	37	20	18	38	12	7	19	7	4	11	14	8	22
P_3 Max	14	12	26	17	24	47	20	20	40	10	5	15	7	5	12	14	9	23
P_3 Perp	14	12	26	17	24	47	20	20	40	10	5	15	7	5	12	14	9	23
P_4 M-D	14	12	26	18	24	48	20	20	40	11	8	19	7	4	11	14	9	23
P_4 B-L	14	12	26	18	24	48	20	20	40	11	8	19	7	4	11	14	9	23
M_1 M-D	14	12	26	33	40	92	20	20	40	12	10	22	7	5	12	14	9	23
M_1 B-L	14	12	26	34	39	91	20	20	40	12	10	22	7	5	12	14	9	23
M_2 M-D	14	12	26	17	25	49	20	20	40	12	10	22	7	5	12	13	9	22
M_2 B-L	14	12	26	17	26	50	20	20	40	12	10	22	7	5	12	13	9	22
M_3 M-D	13	12	25	12	13	26	20	20	40	12	10	22	7	5	12	13	9	22
M_3 B-L	13	12	25	12	14	28	20	20	40	12	10	22	7	5	12	13	9	22

Notes: m = males; f = females; m+f = mixed sex sample.

P.troglodytes and G.gorilla data from Pilbeam (1969). P.paniscus data from Johanson (1974). Hylobates data were provided by T.Harrison. Pongo data are personal measurements taken on British Museum (Natural History) Zoology Department specimens.

Measurements are as defined in Chapter 1.

Table 2.2: Coefficients of variation in extant hominoids (Table 2.1) showing the values for each sex; for a mixed sex sample; and the maximum value encountered in the single sex samples where these exceed the mixed sex sample value.

	P.troglodytes				P.paniscus				C.gorilla			
	m	f	m+f	max	m	f	m+f	max	m	f	m+f	max
I^1 M-D	-	-	-	-	8.74	6.73	-	-	-	-	-	-
I^1 B-L	-	-	-	-	7.59	5.26	-	-	-	-	-	-
I^2 M-D	-	-	-	-	8.86	8.86	-	-	-	-	-	-
I^2 B-L	-	-	-	-	8.22	5.63	-	-	-	-	-	-
C^1 Max	8.81	4.70	13.15	-	8.11	5.56	-	-	6.46	5.66	20.00	-
C^1 Perp	12.02	3.72	14.26	-	9.09	5.80	-	-	6.70	7.07	19.13	-
P^3 M-D	6.89	5.41	6.43	6.89	8.11	5.56	-	-	6.61	5.67	6.99	-
P^3 B-L	5.06	5.60	5.19	5.60	6.45	4.35	-	-	6.67	6.41	6.98	-
P^4 M-D	4.55	4.01	4.22	4.55	7.94	8.20	-	-	4.96	6.43	6.11	-
P^4 B-L	3.44	2.66	3.52	-	6.67	4.55	-	-	4.85	6.51	6.28	6.51
M^1 M-D	5.35	5.39	5.26	5.39	5.56	5.56	-	-	5.74	5.26	6.05	-
M^1 B-L	4.22	5.26	4.64	5.26	5.00	5.00	-	-	5.89	5.27	6.20	-
M^2 M-D	6.40	5.92	6.11	6.40	6.74	6.67	-	-	6.25	6.21	7.27	-
M^2 B-L	4.36	5.68	5.04	5.68	6.86	4.95	-	-	5.41	5.76	6.38	-
M^3 M-D	6.29	6.55	6.34	6.55	6.10	10.00	-	-	6.46	7.38	8.27	-
M^3 B-L	9.11	5.43	7.44	9.11	5.15	6.32	-	-	6.36	7.84	7.66	7.84
I_1 M-D	-	-	-	-	9.46	9.72	-	-	-	-	-	-
I_1 B-L	-	-	-	-	7.14	4.41	-	-	-	-	-	-
I_2 M-D	-	-	-	-	8.00	10.96	-	-	-	-	-	-
I_2 B-L	-	-	-	-	5.63	4.35	-	-	-	-	-	-
C_1 Max	9.68	4.70	11.87	-	7.00	7.95	-	-	7.57	6.77	18.15	-
C_1 Perp	8.29	4.41	11.55	-	5.26	10.77	-	-	6.45	6.39	16.65	-
P_3 Max	5.42	3.68	4.60	5.42	6.17	4.88	-	-	5.71	5.72	9.98	-
P_3 Perp	8.56	5.76	8.41	8.56	16.22	12.86	-	-	9.29	9.04	11.41	-
P_4 M-D	8.34	3.60	6.86	8.34	5.63	11.43	-	-	5.84	5.02	6.71	-
P_4 B-L	5.12	5.32	5.20	5.32	8.97	7.89	-	-	4.79	8.47	7.49	8.47
M_1 M-D	5.68	5.03	5.37	5.68	4.08	6.12	-	-	3.89	4.23	4.79	-
M_1 B-L	6.01	4.78	5.48	6.01	5.62	6.82	-	-	3.56	5.86	5.48	5.86
M_2 M-D	6.12	4.50	5.41	6.12	6.12	5.88	-	-	6.00	4.99	6.52	-
M_2 B-L	6.34	5.39	6.01	6.34	6.52	6.59	-	-	3.93	8.19	7.01	8.19
M_3 M-D	7.40	3.47	5.99	7.40	4.44	6.59	-	-	5.68	7.00	8.00	-
M_3 B-L	6.34	3.51	5.51	6.74	4.76	6.98	-	-	5.35	7.61	7.50	7.61

Table 2.2 continued

P.pygmaeus				H.syndactylus				H.lar				
m	f	m+f	max	m	f	m+f	max	m	f	m+f	max	
7.24	6.47	8.89	-	9.92	9.41	9.30	9.92	8.57	5.21	7.64	8.57	I^1 M-D
7.55	6.08	10.34	-	4.66	7.71	5.89	7.71	12.83	7.66	11.56	12.83	I^1 B-L
7.26	5.75	8.14	-	5.75	6.12	5.86	6.12	8.62	2.60	8.42	8.62	I^2 M-D
11.36	7.77	12.11	-	3.78	5.20	4.27	5.20	10.16	6.36	9.05	10.16	I^2 B-L
5.69	10.51	16.20	-	8.93	14.21	11.86	14.21	6 03	7.86	7.26	7.86	C^1 Max
10.87	10.79	17.55	-	8.59	5.45	10.40	-	9.36	3.61	7.81	9.36	C^1 Perp
5.62	7.06	7.43	-	5.05	9.06	6.66	9 06	4.33	6.73	5.42	6.73	P^3 M-D
5.63	5.52	7.53	-	4.66	5.81	5.05	5.81	5.48	5.82	5.59	5.82	P^3 B-L
9.94	6.53	10.71	-	6.69	8.02	7.30	8.02	6.83	7.90	7.09	7.90	P^4 M-D
8.26	4.42	8.22	8.26	3.81	7.27	5.34	7.27	4.81	5.75	5.11	5.75	P^4 B-L
4.27	3.09	6.83	-	6.50	6.89	6.46	6.89	3.83	6.01	4.83	6.01	M^1 M-D
3.26	2.66	6.34	-	3.75	3.56	3.50	3.75	4.41	3.29	3.95	4.41	M^1 B-L
5.72	4.54	9.22	-	4.86	5.38	5.05	5.38	3.09	7.42	5.15	7.42	M^2 M-D
4.19	3.33	7.31	-	3.41	5.06	3.96	5.06	4.14	4.46	4.17	4.46	M^2 B-L
8.06	9.22	13.19	-	10.21	11.02	10.51	11.02	9 17	12.73	10.48	12.73	M^3 M-D
4.22	5.76	7.42	-	7.03	7.53	7.00	7.53	6.80	7.26	6.90	7.26	M^3 B-L
8.39	8.48	10.36	-	1.75	6.57	5.14	6.57	4.67	6.16	5.19	6.16	I_1 M-D
7.03	7.73	8.80	-	6.34	3.85	5.62	6.34	6.97	9.45	8.05	9.45	I_1 B-L
9.82	8.87	10.11	-	13.09	9.49	11.78	13.09	8.61	8.73	8.49	8.73	I_2 M-D
10.72	6.31	10.16	10.72	9.64	2.53	7.99	9.64	10.28	5.93	8.88	10.28	I_2 B-L
9.97	10.51	13.86	-	4.13	5.37	4.68	5.37	6.75	4.76	6.35	6.75	C_1 Max
10.58	5.35	19.47	-	10.48	5.55	10.16	10.48	5.87	6.95	6.42	6.95	C_1 Perp
7.11	16.27	12.67	16.27	5.46	9.03	7.62	9.03	5.32	4.08	4.78	5.32	P_3 Max
5.02	7.74	9.19	-	5.18	7.95	6.19	7.95	6.49	6.74	6.83	-	P_3 Perp
4.63	9.99	10.65	-	4.40	14.05	8.54	14.05	6.34	8.94	7.27	8.94	P_4 M-D
5.78	6.44	10.90	-	5.94	6.45	5.82	6.45	7.40	6.85	7.14	7.40	P_4 B-L
3.61	4.35	5.92	-	7.49	8.85	7.69	8.85	4.68	5.05	5.05	-	M_1 M-D
4.27	3.50	6.56	-	6.11	8.20	6.69	8.20	5.19	5.78	5.44	5.78	M_1 B-L
3.95	4.59	8.22	-	4.96	8.07	6.13	8.07	3.78	6.04	4.70	6.04	M_2 M-D
4.61	4.77	7.95	-	4.64	6.59	5.39	6.59	4.59	6.17	5.16	6.17	M_2 B-L
4.45	8.78	9.98	-	11.95	9.84	10.70	11.95	7.48	6.25	6.87	7.48	M_3 M-D
3.59	7.02	8.74	-	8.70	5.51	7.64	8.70	4.75	5.39	4.96	5.39	M_3 B-L

Table 2.3: The maximum coefficients of variation encountered in Hominoidea (Table 2.2).

	Max (taxon) Table 2.2	Kay (1982) Max	Best Maximum
I^1 M-D	8.89 (P.pygmaeus)	11.7	11.7
I^1 B-L	12.83 (H.lar)	13.9	13.9
I^2 M-D	8.86 (P.paniscus)	-	8.9
I^2 B-L	12.11 (P.pygmaeus)	-	12.2
C^1 Max	20.00 (G.gorilla)	20.5	20.5
C^1 Perp	19.13 (G.gorilla)	19.9	19.9
P^3 M-D	8.11 (P.paniscus)	9.1	9.1
P^3 B-L	7.53 (P.pygmaeus)	9.0	9.0
P^4 M-D	10.71 (P.pygmaeus)	8.3	10.8
P^4 B-L	8.26 (P.pygmaeus)	7.3	8.3
M^1 M-D	6.83 (P.pygmaeus)	6.5	6.9
M^1 B-L	6.34 (P.pygmaeus)	6.4	6.4
M^2 M-D	9.22 (P.pygmaeus)	8.1	9.3
M^2 B-L	7.31 (P.pygmaeus)	9.1	9.1
M^3 M-D	13.19 (P.pygmaeus)	9.2	13.2
M^3 B-L	9.11 (P.troglodytes)	10.7	10.7
I_1 M-D	10.36 (P.pygmaeus)	-	10.4
I_1 B-L	9.45 (H.lar)	-	9.5
I_2 M-D	10.96 (P.paniscus)	-	11.0
I_2 B-L	10.72 (P.pygmaeus)	-	10.8
C_1 Max	18.15 (G.gorilla)	17.9	18.2
C_1 Perp	19.47 (P.pygmaeus)	19.1	19.5
P_3 Max	16.27 (P.pygmaeus)	10.4	16.3
P_3 Perp	16.22 (P.paniscus)	10.9	16.3
P_4 M-D	11.43 (P.paniscus)	7.3	11.5
P_4 B-L	10.90 (P.pygmaeus)	8.4	10.9
M_1 M-D	6.12 (P.paniscus)	6.1	6.2
M_1 B-L	6.82 (P.paniscus)	6.4	6.9
M_2 M-D	8.22 (P.pygmaeus)	6.7	8.3
M_2 B-L	8.19 (G.gorilla)	7.3	8.2
M_3 M-D	9.98 (P.pygmaeus)	8.7	10.0
M_3 B-L	8.74 (P.pygmaeus)	9.5	9.5

Notes: The first column shows the maximum coefficient of variation encountered for each tooth dimension for the species listed in Table 2.2 with the exception of H.syndactylus which was excluded from this analysis as the sample was small (see Table 2.1). The taxon in which the maximum value was found is in parantheses. The second column lists the maximum CV reported by Kay (1982) for the hominoids which he sampled.

The final column is the best estimate for the maximum CV for each dental measurement for H mi idea based on Table 2.2 and Kay (1982).

3. Range, and range as a percentage of the mean

Fossil samples are often very small for any tooth type and/or fossil site. Coefficients of variation are sample size dependent and when large samples for extant species are compared with small fossil samples then discrepancies between the CV values may result from these differences rather than from more than one species being involved in the fossil sample. This factor may explain the recognition of two species at Rain Ravine, Macedonia by Kay (1982b) as sample sizes are small. In such cases the range of measurements in the fossil sample is the only valid measurement of variation, and this should be compared to the range of values found in modern species. Ranges of values found in the samples of modern hominoids are shown in Table 2.4. These are employed in Chapter 3 for the definition of fossil species. It should be noted that small samples of fossils will tend to underestimate the range, which will have the effect of underestimating the number of species present, the opposite to the CV bias. Due to the fact that relatively small numbers of hominoid species are alive today it may not be possible to find an extant species of a size similar to that in the fossil sample. Even if this is possible then the living species which happens to be the same size as the fossil species may not provide a representative range of variation for hominoids generally.

A possible way around this problem is to convert the range to a size independent measurement. If the range is expressed as a percentage of the mean then this value may be compared between species of differing

size, and provides a useful alternative to CV for small fossil samples. It has the advantage that the sexual composition of the sample is not so critical as it is for CV. This index was calculated for lengths and breadths of each of the upper and lower C - M3 (Table 2.5) for the extant great apes with sample sizes as shown in Table 2.1. Each of the 3 species provides 24 values for this index. These values were regressed on the CV for the same measurement in the same sample for the total of 72 data points. The correlation coefficient is 0.93 which confirms that the range/mean index is in some way comparable to CV when large samples are considered. Data for fossil samples will be assessed against the data in Table 2.5 in addition to CV data in order to remove some of the influence of sample size on the interpretation of variance.

Table 2.4: The mean and the range of dental measurements for the hominoid samples in Table 2.1.

	P.troglodytes			P.paniscus			G.gorilla		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
I^1 M-D	-	-	-	10.4	8.9	11.9	-	-	-
I^1 B-L	-	-	-	7.7	6.8	9.2	-	-	-
I^2 M-D	-	-	-	7.9	6.9	10.1	-	-	-
I^2 B-L	-	-	-	7.2	6.3	8.5	-	-	-
C^1 Max	12.7	10.5	15.6	10.0	8.2	13.3	17.8	12.5	23.2
C^1 Perp	10.0	8.2	13.2	7.8	6.3	10.7	13.6	10.1	17.8
P^3 M-D	7.2	6.3	8.0	7.3	6.2	8.4	10.5	9.2	12.2
P^3 B-L	10.5	9.4	11.8	9.2	8.3	10.3	15.2	13.0	17.1
P^4 M-D	7.0	6.6	7.6	6.2	5.0	7.6	10.8	9.5	12.2
P^4 B-L	10.2	9.5	10.8	8.9	7.7	10.3	14.9	12.6	16.8
M^1 M-D	9.9	9.0	10.6	9.0	7.9	10.3	14.4	12.7	16.7
M^1 B-L	11.2	9.9	11.7	10.0	8.7	11.3	15.2	13.3	17.4
M^2 M-D	10.1	9.0	11.3	9.0	7.8	10.5	15.4	13.4	17.9
M^2 B-L	11.6	10.2	12.8	10.1	9.2	12.1	16.1	14.0	18.3
M^3 M-D	9.1	8.2	10.3	8.1	7.1	9.6	14.4	12.0	17.0
M^3 B-L	11.0	8.8	12.2	9.6	8.8	11.3	15.3	13.0	17.2
I_1 M-D	-	-	-	7.3	5.6	8.7	-	-	-
I_1 B-L	-	-	-	6.9	6.2	8.1	-	-	-
I_2 M-D	-	-	-	7.4	5.2	9.0	-	-	-
I_2 B-L	-	-	-	7.0	6.3	8.4	-	-	-
C_1 Max	12.2	10.3	15.3	9.3	7.5	11.4	15.7	11.3	20.2
C_1 Perp	9.8	8.0	12.2	7.0	5.8	8.9	12.3	9.1	15.5
P_3 Max	11.1	10.2	12.1	8.2	7.1	9.3	16.2	13.7	18.6
P_3 Perp	7.8	7.0	9.8	7.2	5.2	9.7	11.2	8.2	13.8
P_4 M-D	7.7	6.8	9.0	7.0	5.4	9.1	11.2	9.8	13.0
P_4 B-L	8.9	8.0	9.8	7.7	5.6	9.2	12.9	10.5	14.4
M_1 M-D	10.6	9.8	12.2	9.8	8.5	11.9	15.3	13.6	16.8
M_1 B-L	9.7	8.8	11.0	8.8	7.4	9.8	13.2	11.6	14.4
M_2 M-D	11.0	10.2	12.6	10.0	8.3	11.4	16.7	14.7	19.2
M_2 B-L	10.6	9.5	12.3	9.1	7.7	10.5	15.0	12.8	16.8
M_3 M-D	10.3	9.2	11.6	9.1	8.3	10.6	16.9	14.2	19.2
M_3 B-L	10.1	9.4	11.4	8.5	7.4	9.4	14.8	12.4	17.5

Notes: Min = the minimum value encountered; Max = the maximum value encountered.

Table 2.4 continued.

P.pygmaeus			H.syndactylus			H.lar			
Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	
13.6	11.7	15.7	5.2	4.7	6.0	4.8	4.2	5.5	I^1 M-D
12.0	9.6	14.3	4.4	4.0	4.8	3.8	3.3	5.4	I^1 B-L
8.6	7.3	9.7	4.3	3.9	4.8	4.0	3.6	4.8	I^2 M-D
8.6	6.9	11.2	4.9	4.6	5.3	4.0	3.3	5.1	I^2 B-L
15.0	10.3	18.0	8.6	6.8	10.5	7.5	6.7	8.7	C^1 Max
11.9	8.3	15.7	5.9	5.0	7.1	5.3	4.5	6.0	C^1 Perp
9.6	8.1	10.9	5.6	4.8	6.1	4.7	4.2	5.2	P^3 M-D
12.5	10.8	14.2	6.1	5.5	6.7	5.0	4.6	5.5	P^3 B-L
9.5	8.0	12.8	5.5	4.7	6.0	4.3	3.8	5.0	P^4 M-D
12.7	10.0	14.1	6.6	5.9	7.1	5.4	4.8	6.0	P^4 B-L
11.9	10.7	13.4	7.5	6.7	8.1	5.7	5.3	6.2	M^1 M-D
13.1	11.8	14.8	7.3	6.9	7.7	6.2	5.9	7.0	M^1 B-L
12.1	10.4	14.4	8.0	7.4	8.7	6.1	5.6	6.7	M^2 M-D
13.7	12.2	15.3	8.1	7.6	8.6	6.5	6.1	7.0	M^2 B-L
11.2	8.5	13.8	6.9	5.5	8.4	5.3	4.2	6.2	M^3 M-D
13.3	10.9	15.0	7.8	7.1	8.6	6.1	5.2	6.7	M^3 B-L
9.1	7.4	10.5	3.3	3.0	3.5	3.2	2.9	3.5	I_1 M-D
9.7	8 0	11.3	4.0	3.7	4.5	3.5	2.9	3.9	I_1 B-L
8.8	7.0	10.1	3.9	3.4	5.0	3.4	2.9	4.0	I_2 M-D
9.9	8.6	12.3	4.6	4.0	5.2	3.9	3.5	4.5	I_2 B-L
14.1	10.6	17.6	7.8	7.2	8.3	6.8	6.1	7.7	C_1 Max
10.6	7.6	14.2	5.9	5.3	7.5	4.9	4.3	5.5	C_1 Perp
13.6	9.6	15.6	8.4	7.1	9.5	6.7	6.2	7.3	P_3 Max
10.0	8.2	11.3	4.9	4.3	5.3	4.0	3.6	4.5	P_3 Perp
10.4	8.4	11.7	6.5	5.0	7.1	5.2	4.6	5.9	P_4 M-D
11.4	9.3	13.3	4.9	4.4	5.2	4.2	3.8	5.1	P_4 B-L
12.8	11.1	14.1	7.7	6.9	8.7	6.1	5.3	6.6	M_1 M-D
11.9	10.6	13.3	6.1	5.4	6.8	5.0	4.5	5.7	M_1 B-L
13.5	11.7	15.4	8.5	7.5	9.1	6.2	5.4	6.6	M_2 M-D
12.6	11.1	14.3	6.7	6.1	7.4	5.4	4.9	6.0	M_2 B-L
13 3	11.0	15.6	8.2	6.5	9.5	6.1	5.4	7.0	M_3 M-D
11.9	9.8	13.5	6.5	5.2	7.0	5.3	4.8	5.9	M_3 B-L

Table 2.5: Range/mean values for the extant hominoids (samples as in Table 2.1).

	P.troglodytes	P.paniscus	G.gorilla	P.pygmaeus	H.lar
I^1 M-D	-	0.19	-	0.29	0.27
I^1 B-L	-	0.31	-	0.39	0.55
I^2 M-D	-	0.41	-	0.28	0.30
I^2 B-L	-	0.31	-	0.49	0.45
C^1 Max	0.40	0.51	0.60	0.51	0.27
C^1 Perp	0.50	0.56	0.57	0.62	0.28
P^3 M-D	0.24	0.30	0.29	0.29	0.21
P^3 B-L	0.23	0.22	0.27	0.27	0.18
P^4 M-D	0.14	0.42	0.25	0.51	0.28
P^4 B-L	0.13	0.29	0.28	0.32	0.22
M^1 M-D	0.16	0.27	0.28	0.23	0.16
M^1 B-L	0.16	0.26	0.27	0.23	0.18
M^2 M-D	0.23	0.30	0.29	0.33	0.18
M^2 B-L	0.22	0.29	0.27	0.23	0.14
M^3 M-D	0.23	0.31	0.35	0.47	0.38
M^3 B-L	0.22	0.26	0.27	0.31	0.25
I_1 M-D	-	0.42	-	0.34	0.44
I_1 B-L	-	0.28	-	0.34	0.29
I_2 M-D	-	0.51	-	0.35	0.32
I_2 B-L	-	0.30	-	0.37	0.26
C_1 Max	0.41	0.42	0.57	0.50	0.24
C_1 Perp	0.43	0.44	0.52	0.62	0.24
P_3 Max	0.17	0.27	0.30	0.44	0.16
P_3 Perp	0.36	0.63	0.50	0.31	0.23
P_4 M-D	0.29	0.53	0.29	0.32	0.25
P_4 B-L	0.20	0.47	0.30	0.35	0.31
M_1 M-D	0.23	0.35	0.21	0.23	0.21
M_1 B-L	0.23	0.27	0.21	0.23	0.24
M_2 M-D	0.22	0.29	0.27	0.27	0.19
M_2 B-L	0.17	0.31	0.27	0.25	0.20
M_3 M-D	0.23	0.25	0.30	0.35	0.26
M_3 B-L	0.20	0.24	0.34	0.31	0.21

4. Sexual dimorphism indices

The most accurate measurement of sexual dimorphism is a comparison of the mean value in males with the mean value in females. An index of male mean/female mean has been developed from Garn et al, (1973: Martin, 1981), and data for this index in modern hominoids are shown in Table 2.6. These data confirm that dimorphism is greatest in canines and the lower third premolar and least in the cheek teeth. In terms of canine teeth Gorilla is the most dimorphic, next is Pongo, then Pan paniscus and Pan troglodytes, and least dimorphic are the gibbons. Gorilla shows some dimorphism in molars, but the orang-utan shows at least 10% dimorphism in molar dimensions.

The largest specimen in any sample, fossil or modern, is likely to be a male and the smallest specimen is likely to be a female. This is the case for almost every dimension in modern hominoids. An index has been devised which compares the maximum male value with the minimum female value for dental dimensions in extant hominoids and the values for this index are shown in Table 2.7. The index is not really an expression of dimporphism but measures the extent to which the whole sample can vary by comparing the extreme points of the species range. These data can be used to assess the maximum variability present in extant species, and this can be used to test whether the largest and smallest specimen in a fossil sample are within the limits of single extant species or whether they are more different than any modern hominoid. This method does not definitely identify the number of species present but has the advantage that even two teeth from a site

can be shown to be too different in size to be considered to be one species, which makes it a useful addition to the techniques by which variance in fossil hominoids is analysed.

A similar index can be calculated comparing the largest female with the smallest male value (Table 2.8). This index has no value with regard to the fossil data except in that it is a simple numerical expression of the extent to which the male and the female ranges for any dimension overlap. A value greater than unity for this index means that there is no overlap between the ranges although even values just less than unity may also result in bimodal distributions. As has been previously reported canines are the most bimodally and discontinuously distributed teeth in the great apes, although lower canines are not bimodal in Pan paniscus. The high dimorphism in Pongo molars (Table 2.6) is reflected in the discontinuous distributions of 2 molar dimensions and the bimodal distribution of almost all of the molar dimensions. Although the samples are small (12 males, 10 females) they are certainly comparable, and usually larger, than the samples of fossil specimens. It is commonly accepted (e.g. Andrews and Tobien, 1977; Kay, 1982b) that a bimodal distribution of even small samples of fossil molars means that at least two species must be present. The data in Table 2.8 show that this is not a reliable assumption. Even the least variable teeth (first molars) may show bimodal distributions (Figure 2.2), particulary when small samples are being considered.

Table 2.6: Sexual dimorphism index in living hominoids (see Table 2.1 for sample sizes). Index = male mean/female mean.

	P.troglodytes	P.paniscus	G.gorilla	P.pygmaeus	H.syndactylus	H.lar
I^1 M-D	-	0.99	-	1.13	0.98	1.02
I^1 B-L	-	1.04	-	1.16	1.00	1.05
I^2 M-D	-	1.00	-	1.10	1.02	1.08
I^2 B-L	-	1.03	-	1.15	1.02	1.03
C^1 Max	1.24	1.23	1.46	1.34	1.11	1.07
C^1 Perp	1.22	1.28	1.43	1.32	1.17	1.02
P^3 M-D	1.04	1.03	1.07	1.09	0.98	1.04
P^3 B-L	1.00	1.01	1.05	1.11	0.97	1.02
P^4 M-D	1.00	1.03	1.05	1.13	1.06	1.00
P^4 B-L	1.00	1.02	1.06	1.10	1.00	1.00
M^1 M-D	1.01	1.00	1.05	1.12	1.03	1.04
M^1 B-L	1.00	1.00	1.05	1.12	1.00	1.02
M^2 M-D	1.02	0.99	1.08	1.16	1.03	1.03
M^2 B-L	1.03	1.01	1.07	1.13	1.00	1.00
M^3 M-D	1.02	1.03	1.09	1.23	0.94	1.02
M^3 B-L	1.01	1.02	1.06	1.12	0.97	1.02
I_1 M-D	-	1.03	-	1.14	1.03	1.00
I_1 B-L	-	1.03	-	1.10	1.03	1.03
I_2 M-D	-	1.03	-	1.10	1.03	1.00
I_2 B-L	-	1.03	-	1.10	1.00	1.05
C_1 Max	1.18	1.14	1.39	1.20	1.04	1.05
C_1 Perp	1.19	1.17	1.37	1.45	1.11	1.04
P_3 Max	0.99	0.99	1.17	1.18	1.07	1.00
P_3 Perp	1.08	1.06	1.16	1.17	1.02	1.05
P_4 M-D	1.04	1.01	1.08	1.18	1.05	1.00
P_4 B-L	1.02	1.03	1.07	1.21	1.00	1.02
M_1 M-D	1.02	1.00	1.05	1.09	1.00	1.03
M_1 B-L	1.02	1.01	1.05	1.11	1.00	1.02
M_2 M-D	1.02	0.96	1.07	1.15	1.01	1.00
M_2 B-L	1.03	1.01	1.08	1.14	0.99	1.02
M_3 M-D	1.03	0.99	1.10	1.16	1.01	0.98
M_3 B-L	1.02	0.98	1.08	1.15	0.96	1.00

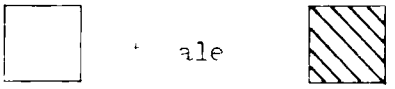
Table 2.7: Index of the maximum variation which occurs in extant hominoids (samples as in Table 2.1). Index = maximum value observed in the (male) sample/the minimum value observed in the (female) sample.

	P.troglodytes	P.paniscus	G.gorilla	P.pygmaeus	H.syndactylus	H.lar
I^1 M-D	-	1.32	-	1.34	1.28	1.28
I^1 B-L	-	1.35	-	1.49	1.20	1.64
I^2 M-D	-	1.30	-	1.33	1.23	1.33
I^2 B-L	-	1.33	-	1.62	1.13	1.46
C^1 Max	1.49	1.62	1.86	1.75	1.54	1.30
C^1 Perp	1.61	1.70	1.76	1.89	1.42	1.20
P^3 M-D	1.27	1.35	1.33	1.35	1.27	1.24
P^3 B-L	1.15	1.24	1.32	1.31	1.10	1.20
P^4 M-D	1.15	1.52	1.28	1.60	1.28	1.26
P^4 B-L	1.13	1.34	1.33	1.28	1.17	1.18
M^1 M-D	1.14	1.25	1.31	1.25	1.17	1.17
M^1 B-L	1.18	1.30	1.31	1.25	1.10	1.19
M^2 M-D	1.26	1.35	1.34	1.38	1.18	1.16
M^2 B-L	1.25	1.32	1.31	1.25	1.12	1.15
M^3 M-D	1.23	1.24	1.42	1.62	1.23	1.48
M^3 B-L	1.22	1.25	1.32	1.38	1.19	1.29
I_1 M-D	-	1.55	-	1.42	1.17	1.21
I_1 B-L	-	1.31	-	1.41	1.18	1.34
I_2 M-D	-	1.60	-	1.38	1.47	1.38
I_2 B-L	-	1.31	-	1.41	1.16	1.29
C_1 Max	1.49	1.52	1.79	1.66	1.15	1.26
C_1 Perp	1.53	1.47	1.70	1.87	1.42	1.28
P_3 Max	1.14	1.19	1.36	1.63	1.34	1.16
P_3 Perp	1.40	1.87	1.68	1.38	1.21	1.25
P_4 M-D	1.29	1.43	1.33	1.39	1.42	1.28
P_4 B-L	1.23	1.64	1.37	1.43	1.16	1.34
M_1 M-D	1.24	1.22	1.24	1.27	1.23	1.25
M_1 B-L	1.25	1.31	1.24	1.25	1.20	1.27
M_2 M-D	1.24	1.18	1.31	1.32	1.19	1.20
M_2 B-L	1.29	1.36	1.31	1.29	1.09	1.22
M_3 M-D	1.22	1.14	1.35	1.42	1.22	1.30
M_3 B-L	1.19	1.27	1.41	1.38	1.10	1.23

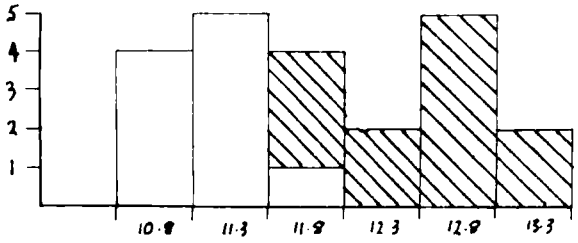
Table 2.8: Sexual overlap index in living hominoids (samples as in Table 2.1). The index = male minimum/female maximum. Values greater than unity mean that the male and the female ranges do not overlap. The higher the value for indices below unity the more bimodal the distribution.

	P.troglodytes	P.paniscus	G.gorilla	P.pygmaeus	H.syndactylus	H.lar
I^1 M-D	-	0.77	-	0.81	0.78	0.84
I^1 B-L	-	0.85	-	0.93	0.88	0.85
I^2 M-D	-	0.68	-	0.92	0.91	0.92
I^2 B-L	-	0.87	-	0.89	0.89	0.79
C^1 Max	0.98	0.98	1.19	1.03	0.84	0.88
C^1 Perp	0.94	1.00	1.05	0.86	1.00	0.80
P^3 M-D	0.85	0.85	0.85	0.89	0.85	0.83
P^3 B-L	0.80	0.82	0.85	0.88	0.82	0.84
P^4 M-D	0.89	0.86	0.87	0.90	0.86	0.76
P^4 B-L	0.89	0.82	0.90	0.79	0.87	0.80
M^1 M-D	0.85	0.81	0.88	0.99	0.84	0.88
M^1 B-L	0.89	0.79	0.89	1.04	0.90	0.91
M^2 M-D	0.86	0.78	0.86	1.00	0.88	0.88
M^2 B-L	0.89	0.82	0.83	1.01	0.90	0.90
M^3 M-D	0.80	0.78	0.83	0.89	0.65	0.76
M^3 B-L	0.73	0. 5	0.77	0.97	0.84	0.80
I_1 M-D	-	0.72	-	0.84	0.91	0.86
I_1 B-L	-	0.84	-	0.88	0.90	0.77
I_2 M-D	-	0.70	-	0.74	0.83	0.77
I_2 B-L	-	0.89	-	0.82	0.85	0.86
C_1 Max	0.95	0.80	1.03	1.01	0.93	0.87
C_1 Perp	0.96	0.76	1.04	1.13	0.93	0.87
P_3 Max	0.86	0.79	0.92	0.83	0.87	0.87
P_3 Perp	0.86	0.69	0.90	0.96	0.85	0.86
P_4 M-D	0.86	0.67	0.87	0.89	0.90	0.84
P_4 B-L	0.85	0.76	0.85	0.96	0.85	0.85
M_1 M-D	0.89	0.76	0.90	0.98	0.80	0.92
M_1 B-L	0.84	0.82	0.89	1.00	0.87	0.91
M_2 M-D	0.87	0.73	0.86	0.99	0.86	0.86
M_2 B-L	0.83	0.81	0.88	0.98	0.82	0.86
M_3 M-D	0.87	0.78	0.88	0.96	0.68	0.82
M_3 B-L	0.88	0.86	0.87	0.98	0.74	0.91

Figure 2.2: Frequency histograms for first and third dimensions in Pongo pygmaeus

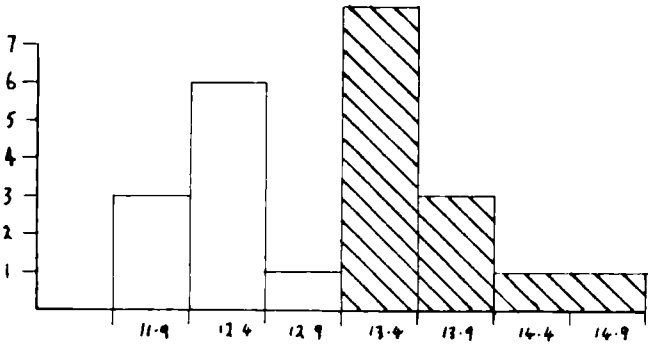


M^1 M-D length



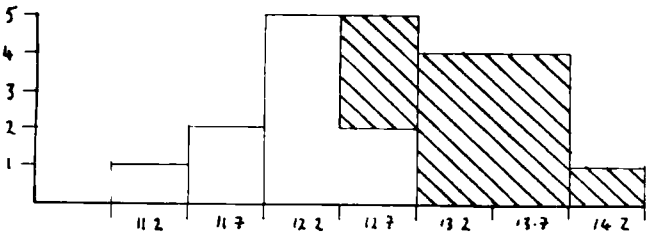
Categories
11.6 - 11.
11.1 - 11.5
11.6 - 12.
12.1 - 12.5
12.6 - 13.0
13.1 - 13.5

M^1 M-D breadth



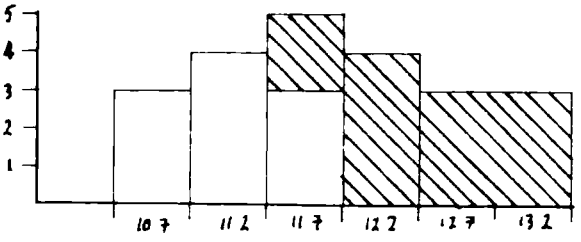
Categories
11.7 - 12.1
12.2 - 12.6
12.7 - 13.1
13.2 - 13.6
13.7 - 14.1
14.2 - 14.6
14.7 - 15.1

M_1 M-D length



Categories
11.0 - 11.4
11.5 - 11.9
12.0 - 12.4
12.5 - 12.9
13. - 13.4
13.5 - 13.9
14. - 14.4

M_1 B-I breadth



Categories
10.5 - 1 .
11.0 - 11.4
11.5 - 11
12.0 - 12 4
12.5 - 1
13. - 1 .

5. The identification of sex in fossil specimens

I have suggested above that species would be most easily defined if the sex of specimens could be determined. This would allow the comparison of specimens of the same sex which would be easier to assess in the light of comparative data. A number of the more dimorphic teeth in living hominoids (Table 2.6) were compared to M1 length in males and females in extant hominoids to see how completely sexes could be indentified. Data for Pan troglodytes, Gorilla, Pongo and Hylobates lar were used (Table 2.1). Third molars are quite sexually dimorphic in living hominoids (Table 2.6) but an index of M^3 to M^1 and of M_3 to M_1 do not separate the sexes. The lower third premolar is also a dimorphic tooth but an index of P_3/M_1 does not distinguish males from females to any significant extent.

The means, ranges and sample sizes of C^1/M^1 lengths and C_1/M_1 length are shown in Table 2.9. Since the ranges of the indices vary for the same sex animals of different species the values for any one species should not be used to assess fossil specimens of unknown affinities. By combining these data which sample all of the non-human hominoids it would be reasonable to conclude that when the C^1/M^1 index is greater than 1.40 the specimen is almost certainly a male, when the index is less than 1.13 then the specimen is almost certainly a female. For the C_1/M_1 index a value greater than 1.20 is probably male, a value less than 0.92 is almost certainly a female. This means that the sex of fossil specimens can only be assessed with any certainty in specimens preserving a canine and first molar. The

broad limits of the index which do not defi itely identify male or female hominoids will mean that even fossil specimens preserving the correct teeth may not be clearly identifiable as regards sex.

Table 2.9: Maximum canine length/mesial-distal M1 length in extant hominoids (samples as in Table 2.1).

C^1/M^1

Taxon	Sex	n	Mean	Min	Max
P.troglodytes	Male	14	1.41	1.13	1.62
P.troglodytes	Female	12	1.15	1.04	1.28
G.gorilla	Male	20	1.43	1.26	1.65
G.gorilla	Female	20	1.03	0.93	1.15
P.pygmaeus	Male	12	1.35	1.24	1.53
P.pygmaeus	Female	9	1.13	0.90	1.36
H.lar	Male	13	1.34	1.20	1.51
H.lar	Female	7	1.26	1.12	1.40

C_1/M_1

P.troglodytes	Male	13	1.22	0.98	1.42
P.troglodytes	Female	11	1.06	0.95	1.19
G.gorilla	Male	20	1.16	1.00	1.27
G.gorilla	Female	18	0.87	0.79	0.95
P.pygmaeus	Male	12	1.14	1.02	1.35
P.pygmaeus	Female	7	1.02	0.86	1.17
H.lar	Male	14	1.12	0.92	1.33
H.lar	Female	8	1.12	1.02	1.20

Notes: n = sample size; Min = minimum value observed; Max = maximum value observed.

III. CONCLUSIONS

The coefficient of variation is the best way to identify the least variable, and therefore most useful, tooth dimensions for defining fossil taxa. These are the breadth of M^1 and the length of M_1 in hominoids. In addition, coefficient of variation can draw attention to a fossil sample which appears to exceed the variance in living hominoids, although differences between the composition and sizes of the comparative and fossil samples may account for the discrepancy in CV values. Sample size has the effect of making small samples appear more variable than larger samples of the same taxon when CV is used. Unless the modern sample can be shown to be constituted in exactly the same way, or at least to encompass the possible limits for the constitution of the fossil sample (all males, all females, 1 species, 2 species etc.) the comparison is not valid. Coefficient of variation cannot be used to determine the number of species being sampled nor to confirm that a single species is present in a fossil sample. CV is an indirect and probably poor measurement of sexual dimorphism and should not be used until further justified. In the present work coefficient of variation has been used as one of several methods to assess whether a morphologically homogeneous fossil sample could reasonably be interpreted as representing a single species.

The range of measurements in a fossil sample can be compared to the range of values found in modern species. The range may be expressed as a percentage of the mean value in order to allow comparisons with extant hominoids of different sizes. The use of range, and range

expressed as a percentage of the mean, has the advantage that the sexual composition of the sample is not so critical as it is for CV. It should be noted, however, that small samples tend to understimate the range, which has the effect of underestimating the number of species present. This bias is the opposite of the effect of small samples on CV. Range, and range expressed as a percentage of the mean, were therefore used in addition to CV in the assessment of fossil samples to determine whether the variance was compatible with the variance in modern hominoids.

Sexual dimorphism is best described by a comparison of the mean value in males with the mean value in females of a species. This is of limited value for fossil taxa as it requires the correct identification of the sex of fossil specimens. The largest specimen in any sample, fossil or modern, is likely to be a male and the smallest specimen is likely to be a female. An index has been devised which compares the maximum value with the minimum value. This index measures the extent to which the whole sample varies by comparing the extreme points of the species range. It has the advantage that it can be used to assess whether the largest and smallest specimen in a fossil sample are within the limits of a single extant species, or whether they are more different than any modern hominoid, provided that at least two examples of a tooth type are represented. The disadvantages are the same as those for range; that small samples will be unlikely to represent the extremes of the species range. This will bias the results towards underestimating the number of fossil taxa. This index will be used in conjunction with CV and range to determine

whether a fossil sample can be shown to exceed the variance found in modern hominoid taxa.

A bimodal distribution of dental dimensions of molar teeth has been commonly accepted to mean that at least two species must be represented. Comparative data show that this assumption is not valid, especially for small sampl s. Bimodality and/or non-overlapping ranges will not therefore be accepted as definite evidence for the presence of more than one fossil species in a sample.

It must be remembered that none of these methods separate species of similar dental morphology which show considerable overlap in dental size (e.g. H.syndactylus and H.hoolock). If the later Miocene hominoids were undergoing a radiation then it is probable that the number of species will be underestimated in fossil samples, which inevitably sample considerable periods of time, and often sample a wide geographical range either at present (e.g. Siwaliks) or by the nature of the depositional environment.

No one method of variance analysis in living hominoids can provide definite answers as to numbers of species. The use of one method as entirely objective and reliable (e.g. Kay, 1982b) is misleading. All of the methods discussed above were employed in this work (Chapter 3).

CHAPTER 3

LATER MIOCENE HOMINOIDEA

I. INTRODUCTION

1. Introduction

The aim of this chapter is to establish species and generic groupings of the later Miocene Hominoidea and to describe the morphological and metrical features which characterise them. The relationships of the taxa to one another and to extant hominoids will be assessed in Chapter 6 in the light of new interpretations of species composition, morphology and metrics (this chapter), and of new data and interpretations concerning enamel thickness (Chapter 4) and enamel microstructure (Chapter 5). I begin by reviewing the major publications relating to the taxonomy of later Miocene hominoids with particular emphasis on the first descriptions of fossil material. The literature is reviewed by geographical regions and in blocks of time which are defined according to major taxonomic revisions of the later Miocene hominoids.

2. An historical review of the literature relating to the taxonomy of later Miocene hominoids

(a) European later Miocene Hominoidea (1856 - 1937)

The first fossil pongid dentition was described from the Miocene of France by Lartet (1856) as a new species and genus, Dryopithecus fontani, which he considered to be more closely related to humans than were the extant apes. Two more complete mandibles and several isolated teeth were assigned to this species (Gaudry, 1890; Harle, 1898, 1899; and Deperet, 1911). Gaudry considered that the mandibular

morphology of these specimens contradicted Lartet's hypothesis that D.fontani was more similar to humans than were the apes. The species geographical range was extended when Smith Woodward (1914) referred to it a mandible from the late Miocene of Spain.

During this period several German localities had produced a number of isolated teeth and a complete femur. The teeth fall into two size categories. The smaller teeth have been assigned to a number of species and genera (Schlosser, 1901; Remane,1921; Abel, 1931; Hurzeler, 1954; Simons and Pilbeam, 1965); their affinities with other European fossil forms are currently unclear. The large teeth have also been assigned to a number of taxa (Quenstedt, 1867; Branco, 1897; Schlosser, 1901; Koken, 1905; Abel, 1918-1919), but probably belong to D.fontani as recognised by Simons and Pilbeam (1965).

Four isolated hominoid teeth are known from the Vienna Basin in Czechoslovakia. Three of these were described by Abel (1902). He described a new genus and species, Griphopithecus suessi, and a new species of Dryopithecus, D.darwini. Remane (1921) and Abel (1931) synonymised these taxa and called the species D.darwini as they had decided that the holotype of G.suessi was a deciduous premolar of that species. As the first revisor Remane (1921) was entitled to do this although the trivial name suessi appears earlier in the pub ication (Abel, 1902) than does the name darwini. It must be borne in mind, however, that even if the synonymy has been correctly d termined the generic name Griphopithecus is still available for use if its type species, darwini, were assigned to its own genus, or to a

genus described later than 1902.

(b) Asian later Miocene Hominoidea (1868 - 1937)

Evidence for the previous existence of Anthropoid apes in Indo-Pakistan was first published by Falconer (1868) who had come into possession of a large canine tooth which has subsequently been lost. Lydekker (1879) described a relatively complete maxilla (GSI-D 1) as a new species and genus, Palaeopithecus sivalensis. Because the canine was short, blunt and conical he assumed that this specimen was a female and that Falconer's canine, which was apparently slightly larger, represented a male of the species. Lydekker (1879) suggested that this specimen represented a species slightly larger than the orang-utan, but which showed strong similarities to the chimpanzee, only the small size of P^4 prevented him from assigning the specimen to the same genus as the chimpanzee. Later he (Lydekker, 1886) and Pilgrim (1910b) made this species congeneric with the chimpanzee, but Dubois (1897) and, later, Pilgrim (1913) considered Palaeopithecus sivalensis to be so distinct as to warrant its own genus.

A new genus and species, Sivapithecus indicus (Pilgrim, 1910a) was described for an isolated lower molar (GSI D176) from the tertiary deposits of India. Pilgrim considered the tooth to resemble the M_3 of Gorilla savagei, but to differ in lacking cingula, having low cusps and a shallow buccal groove. An Asian representaive of Dryopithecus, Dryopithecus punjabicus (Pilgrim, 1910a); was made available in the

same paper although a type specimen was not designated.

Pilgrim (1915) reported that new material had confirmed the species which he had described in 1910 but had necessitated two additional new species of Dryopithecus, Dryopithecus chinjiensis and Dryopithecus giganteus, and a new genus and species, Palaeosimia rugosidens. A lectotype (GSI D118 & 119) was designated for D.punjabicus and a maxilla, previously considered to represent a primitive species of Palaeopithecus (Pilgrim, 1913), was referred to D.punjabicus. Pilgrim (1915) compared these specimens with D.fontani, D.rhenanus and D.darwini and concluded that while there was no doubt that the Punjab material should to referred to this genus it was most similar to D.darwini. The two new species of Dryopithecus were seen to resemble D.punjabicus and were referred to Dryopithecus on that basis (Pilgrim, 1915).

Sivapithecus indicus (Pilgrim, 1910a) was discussed under the heading Hominidae as Pilgrim (1915) considered this species to resemble Man more closely than did any other genus, except Pithecanthropus (Dubois, 1893). He suggested that a, hypothetical, closely related form to S.indicus was directly ancestral to Man. Pilgrim (1915) stated that a mandible (GSI D177) had been recovered which undoubtedly belonged to the same species as the Holotype (GSI D176) but which he considered to be a much better representative of S.indicus. He therefore proposed to make this specimen the new "type" for S.indicus. This procedure is not permis ible under the ICZN rules. Later, Pilgrim (1927) and Lewis (1937) both placed the two specimens in separate species, so care must

be taken when reading subsequent papers referrring to the S.indicus "type" specimen.

Several specimens of S.indicus were used to reconstruct the mandible of this species (Pilgrim, 1915). The result was a tooth row which curved in towards the midline in the premolar region. This feature was considered to differentiate Sivapithecus from all other genera, and to show an important link in the descent of Man from the lower Primates. Pilgrim (1915) noted the analagous features in the upper molars of Palaeopithecus and the lower molars of S.indicus, but considered that the reconstructed dental arch shape in Sivapithecus warranted generic distinction. Remane, Schlosser and Lydekker (Remane, 1921) reached the conclusion that the new S.indicus "type" (GSI D177) belonged to Palaeopithecus sivalensis and Remane believed that this species was directly ancestral to the orang-utan.

Three partial mandibles were recovered during an AMNH visit to India and each was designated the holotype of a new species, Dryopithecus pilgrimi, Dryopithecus cautleyi and Dryopithecus frickae, which was also considered to represent a direct lineage (Brown et al, 1924). In the field Brown identified these specimens as Palaeopithecus, but this identification was later rejected as Palaeopithecus was only known from younger beds! Several differences between these specimens and the European species D.fontani were noted. The material was referred to Dryopithecus as it shared the Y5 pattern described by Gregory (1922). Brown et al (1924) clearly regarded all of the Siwalik genera as synonyms of Dryopithecus. They did not necessarily regard their

new species as being more similar to the European forms than they were to the other Siwalik genera. Gregory and Hellman (1926) regarded the entire Siwalik hominoid primate fauna as being allied with the orang-utan rather than with the gorilla-chimp-man group, which they considered to be allied with the European Dryopithecus.

Additional Siwalik hominoid specimens were described by Pilgrim (1927) which confirmed that Gregory's (1922) reconstruction of the S.indicus mandible was more accurate than that of Pilgrim (1915). Pilgrim (1927) recognised that this made Sivapithecus indicus less unique and described three new species; Sivapithecus himalayensis, Sivapithecus orientalis and Sivapithecus middlemissi. The species were differentiated by size, stratigraphic position and minor structural details. A new species Palaeopithecus (?) sylvaticus (Pilgrim, 1927) was described for a mandible whose molars were too broad for Dryopithecus, but which also exhibited (unspecified) morphological differences from Sivapithecus. Pilgrim accepted that the new evidence supported Remane's (1921) belief that Palaeopithecus and Sivapithecus were very closely related but he did not consider them to be ancestral to the orang-utan.

Lewis (1934) prefaced his first article on the Siwalik hominoids by remarking that new finds and more detailed study would lead to a synthesis of the presently recognised species as he considered the distinctions drawn between the isolated fossil teeth were not comparable in magnitude to those drawn between extant species, particularly as sexual differences would undoubtedly be confusing the

problem. Nevertheless he described three new genera and six new species of hominoids!

A new species and genus, Ramapithecus brevirostris (Lewis, 1934), was described as a member of the family Simiidae (?Hominidae) based on a fairly complete maxilla (YPM 13799). The genus was diagnosed as having a parabolic dental arcade, reduced facial prognathism, no diastema, small canines and incisors, and simple molar crowns with low rounded cusps. The genus was distinguished from Sivapithecus by its more crowded dentition and its more hominid-like anterior teeth. A second species, Ramapithecus hariensis was distinguished from the type species by having more rounded molar crowns and less crowded teeth.

A second new genus was described with Sugrivapithecus salmontanus (Lewis, 1934) as the type species. The holotype was the only specimen and the species was defined as having a divergent mandible with a well developed chin, narrow elongate cheek teeth, molarized P_4, small canines and incisors and mesiodistal crowding of the dentition. A second species Sugrivapithecus gregoryi (Lewis, 1936) was later added and was discriminated on the basis of its extreme degree of molar elongation. A third new genus based on Bramapithecus thorpei (Lewis, 1934) was diagnoised as having lower molars which were very short in comparison to their breadth.

A new species, Dryopithecus sivalensis (Lewis, 1934) was described for a specimen (YPM 13806) characterized by a very massive jaw with rather small teeth. Two isolated teeth were also described as

Dryopithecus but Lewis remarked that in both canines and cheek teeth the Indian species of Dryopithecus were well removed from the European species, except for D.darwini. Adaetontherium incognitum (Lewis, 1934) was described as a probable anthropoid primate based on an isolated tooth.

(c) The first taxonomic revision of Eurasion later Miocene hominoids (Lewis, 1937) (Table 3.1)

Until 1937 every major, and many minor, specimens had been described as representing a new species. This had produced an improbably large Siwalik anthropoid fauna comprising nine genera with twenty-two contained species. Lewis (1937) made the first attempt to bring order to the taxonomy of the later Miocene hominoids. He determined synonymy by common morphology, within upper and lower dentitions, and by occlusion, between upper and lower dentitions. For the first time, observations of recent hominoid species were taken into account to allow for individual variation in dimensions and in minor details of morphology. This approach reduced the Siwalik primates to four genera containing ten species (Table 3.1). The four genera which Lewis (1937) recognised were much more specific to the Siwalik primates as species previously assigned to Dryopithecus were referred to, or synonymised with species belonging to Bramapithecus, Ramapithecus, Sivapithecus and Sugrivapithecus.

Bramapithecus comprised three species (Table 3.1), each of which was represented only by the holotype, in each case a mandible. The genus was diagnosed as being of medium size with a relatively shallow, but

Table 3.1: Systematic revision of the Siwalik hominoids (Lewis, 1937).

Lewis (1937) taxa	Species to which the hypodigm had previously been assigned
Bramapithecus thorpei (Lewis, 1934)	B.thorpei (Lewis, 1934)
B.punjabicus (Pilgrim, 1910a)	D.punjabicus (Pilgrim, 1915, partim)
B.sivalensis (Lewis, 1934)	D.sivalensis (Lewis, 1934)
Ramapithecus brevirostris (Lewis, 1934)	R.brevirostris (Lewis, 1934)
Sivapithecus sivalensis (Lydekker, 1879)	Palaeopithecus sivalensis (Lydekker, 1879)
	P.(?) sylvaticus (Pilgrim, 1927)
	Palaeosimia rugsidens (Pilgrim, 1915)
	Sivapithecus indicus (Pilgrim, 1915, partim)
	Ramapithecus hariensis (Lewis, 1934)
	Dryopithecus pilgrimi (Brown et al., 1924)
	D.cautleyi (Brown et al., 1924)
	Dryopithecus sp. (Lewis, 1934)
	D.cautleyi (Lewis, 1934)
	D.punjabicus (Pilgrim, 1915, partim)
	D.chinjiensis (Pilgrim, 1915, partim)
S.indicus (Pilgrim, 1910a)	S.indicus (Pilgrim, 1910a)
	S.himalayensis (Pilgrim, 1927)
	S.middlemissi (Pilgrim, 1927)
	? S.indicus (Pilgrim, 1927)
	S.orientalis (Pilgrim, 1927)
	Dryopithecus frickae (Brown et al., 1924)
	Dryopithecus sp. (Pilgrim, 1927)
	D.chinjiensis (Pilgrim, 1927)
S.giganteus (Pilgrim, 1915)	Pithecus cf. satyrus (Falconer, 1868)
	Dryopithecus giganteus (Pilgrim, 1915)
S.darwini (Abel, 1902) (*)	Griphopithecus suessi (Abel, 1902)
	Dryopithecus darwini (Abel, 1902)
	D.darwini (Remane, 1921; Abel, 1931)
Sugrivapithecus salmontanus (Lewis, 1934)	Palaeopithecus sp. (Pilgrim, 1913)
	Dryopithecus punjabicus (Pilgrim, 1915, partim)
	Sugrivapithecus salmontanus (Lewis, 1934)
	The Sugrivapithecus (sic) (Hrdlicka, 1935)
S.gregoryi (Lewis, 1936)	Sugrivapithecus gregoryi (Lewis, 1936)

Note: (*) indicates a non Siwalik species included for completeness.

very robust, mandibular corpus, having low to medium height tooth crowns with small low cusps. The three species were distinguished on the basis of differences in mandibular robusticity and in the proportion of tooth size compared with jaw size (Lewis, 1937). Ramapithecus became a monospecifc genus (Table 3.1). The type species, R.brevirostris, was diagnosed as for the type description of this genus (Lewis, 1934). Lewis (1937) considered this species to be intermediate in dental morphology between the unspecialized Miocene Pongidae and the Hominidae and Australopithecus (Dart, 1925).

Lewis (1937) formally synonymised Palaeopithecus (Lydekker, 1879) and Sivapithecus (Pilgrim, 1910a). He abandoned the prior name, Palaeopithecus in favour of Sivapithecus (Pilgrim, 1910a) as Palaeopithecus (Lydekker, 1879) is a homonym of Palaeopithecus (Voigt, 1835), a name applied to the stegocephalian footprints of the Butsundstein of Hildurghausen, Saxe-Meiningen, Germany. Palaeopithecus (Voigt, 1835) is itself a synonym of Cheirotherium (Kaup, 1835) but is still not available for use. Four Sivapithecus species were recognised (Table 3.1) and the genus was diagnosed as follows: jaws and cheek teeth large or very large, maxillary arch with a diastema, no mandibular diastema, canines very variable, molars moderately broad with crowns and cusps of medium height, molar cusps swollen so that they converge towards the midline, restricting the occlusal basins, and molar crowns show large basal bulges. Sivapithecus sivalensis became a melting pot for previously described species with small or medium sized canines. It included the holotypes of five species, and also Pilgrim's (1915) alternative type for

S.indicus (Table 3.1). S.indicus was diagnoised by Lewis (1937) as being larger than S.sivalensis, with large and stout canines. The holotypes of four species became junior synonyms of S.indicus in this revision (Table 3.1). S.giganteus (Pilgrim, 1915) was retained by Lewis and he referred D.darwini (Abel, 1902) to Sivapithecus. The two species of Sugrivapithecus were retained and a maxilla, previously referred to D.punjabicus, was referred to the type species, S.salmontanus.

Lewis (1937) referred the Vienna Basin material (Abel, 1902) to Sivapithecus on the basis of its molar crown morphology. Remane (1921) had synonymised D.darwini with G.suessi, and as first revisor had selected the nomen darwini (Abel, 1902) as the trivial name for the species. (ICZN Article 24a). As Griphopithecus was not invalidated by this synonymy, and merely became a junior synonym of Dryopithecus, and has priority over Sivapithecus (Pilgrim, 1910a); Lewis (1937) should properly have referrred the Siwalik species of Sivapithecus (Table 3.1) to the genus Griphopithecus (Abel, 1902), with Sivapithecus becoming a junior synonym of that genus. It has recently been suggested (Szalay and Delson, 1979) that the ICZN should be petitioned to suppress the name Griphopithecus as to correct Lewis' error would cause taxonomic confusion. There is no need to suppress the trivial name suessi as Remane was entitled to make this a junior synonym of darwini as first revisor. Had Lewis (1937) not recognised Griphopithecus as a genus distinct from Dryopithecus the genus Griphopithecus could be suppressed as a nomen oblitum (ICZN 23b). However, since the only reason why Griphopithecus has not been used as

a senior synonym has been the result of Lewis' (1937) error this course is not open. Moreover, if the synonymy of darwini and suessi is maintained then darwini becomes the type species of the genus Griphopithecus and if this hypodigm is considered to be congeneric with Sivapithecus then the genus must be called Griphopithecus. My interpretation of the holotype of G.suessi is described below, but it is sufficient to say that I do not accept the synonymy of suessi and darwini. The species darwini can therefore be referred to the genus Sivapithecus. Any attempt to make the holotype of G.suessi part of the hypodigm of Sivapithecus would require the changing of the genus name to Griphopithecus. This would cause considerable confusion. These problems are best avoided by not assigning the holotype of G.suessi to any hypodigm (see below).

The revision by Lewis (1937) made two substantial contributions to the understanding of the taxonomy of later Miocene hominoids. Firstly, it resulted in a considerable reduction of taxa from the Siwaliks (Table 3.1). Secondly, Lewis (1937) did not recognise the presence of Dryopithecus in Indo-Pakistan. Most of the resemblances of Siwalik specimens to European Dryopithecus had been based on comparison with D.darwini. Lewis (1937) determined that D.darwini was not most closely related to D.fontani, but to Siwalik species of Sivapithecus. Although he did not directly address the D.fontani question he implicity recognised it as a western European species and genus. The four Siwalik genera were entirely recognised from Indo-Pakistan with the exception of Sivapithecus, which had a single species recorded from Eastern Europe. This view was supported by

Gregory et al (1938) who emphasized the distinctiveness of the Siwalik hominoids from western European Dryopithecus. They suggested that all of the Siwalik hominoids, and therefore presumably S.darwini from the Vienna Basin, sampled animals of which the orang-utan was a likely offshoot.

(d) European later Miocene Hominoidea (1937 - 1965)

Material from the Miocene of Spain had been described as D.fontani by Smith-Woodward (1914). A second specimen was assigned to that species by Villalta and Crusafont (1942). This specimen was later redescribed as a new species, Sivapithecus occidentalis (Villalta and Crusafont, 1944), because the authors considered its enamel folding pattern to closely resemble S.sivalensis. A new genus and species was described for a partial mandibular tooth row, this was named Hispanopithecus laietanus (Villalta and Crusafont, 1944). Further material was referred to Hispanopithecus laietanus by Crusafont (1958).

The view that S.occidentalis belonged to the genus Sivapithecus did not receive wide acceptance. Crusafont and Hurzeler (1961) recognised that S.occidentalis and H.laietanus belonged to a single species, for which they used the nomen H.laietanus. In doing so they exercised their right, as first revisors, to select one of two simultaneously published names as the trivial name (ICZN, Article 24a). These authors also described a new species of Dryopithecus, D.piveteaui, and a new genus and species Rahonapithecus sabadellensis (Crusafont and Hurzeler, 1961). They suggested that Rahonapithecus and

Hispanopithecus might only warrant subgeneric status within Dryopithecus. Further material from the Miocene of Spain was described by Crusafont (1965) and Crusafont and Hurzeler (1969) without taxonomic changes. In a description of the Spanish material Crusafont and Golpe-Posse (1973, 1974) provisionally referred a C^1 to S.indicus.

A relatively complete mandible from St.Stefan, Austria was described as a new subspecies, D.fontani carinthiacus (Mottl, 1957). This specimen received little subsequent attention, although it represented the eastern most limit of this species.

A new genus of hominoid was described from the late Miocene of Turkey based on a mandibular fragment and was named Ankarapithecus meteai (Ozansoy, 1957, 1965).

(e) African later Miocene Hominoidea (1937 - 1965)

The presence of hominoids in the later Miocene deposits of Kenya was first reported by Le Gros Clark and Leakey (1950). They suggested that a specimen listed as being from Rusinga Island, as well as two isolated teeth, one of which was undoubtedly from Maboko Island, and therefore Middle Miocene, could not be assigned to Proconsul. The maxilla, originally described by MacInnes (1943) and referred to Proconsul africanus was suggested to closely resemble the Sivapithecus specimens from Indo-Pakistan in having large upper premolars and in lacking molar cingula. Le Gros Clark and Leakey (1950) recognised that the maxilla (M 16649) differed from the Indo-Pakistan examples of Sivapithecus in having a flatter palate and in retaining a lingual cingulum on P^4. They made the specimen the Holotype of a new species, Sivapithecus africanus. A further hominoid specimen was recovered from the Middle Miocene deposits at Fort Ternan, Kenya and a new genus and species, Kenyapithecus wickeri, was described based on the partial maxilla (KNM FT-46) (Leakey, 1962). Leakey believed that Kenyapithecus wickeri was directly ancestral to man, but Simons (1964) argued that Kenyapithecus showed no major differences from Ramapithecus and in fact shared specializations with it.

(f) Asian later Miocene Hominoidea (1937 - 1965)

Von Koenigswald (1935) described a new species and genus, Gigantopithecus blacki based on a right M_3 obtained from a drugstore in China. Weidenreich (1944) described additional material of this species, probably from the Pleistocene of China, which he considered to be a giant ancestor of the middle Pleistocene Homo erectus.

Von Koenigswald (1952) pointed out that these two forms were broadly contemporaneous and concluded that G.blacki represented an extinct form of Hominidae. A complete mandible confirmed the presence of G.blacki in the Pleistocene of China (Woo, 1962).

Pilgrim (1915) described the species D.giganteus based on a very large lower molar. This species was assigned to Sivapithecus by Lewis (1937). Von Koenigswald believed that this species was closely related to G.blacki which he had recently described from China. His reasons for this, other than size, are unclear. Von Koenigswald (1949) did not believe that giganteus should be assigned to Gigantopithecus but instead described a new genus, Indopithecus, with Indopithecus giganteus (Pilgrim, 1915) as the type species. Hooijer (1951) argued that the holotype of this species could not be excluded from S.indicus on the basis of size alone, and that it showed no morphological affinities with Gigantopithecus. A large mandible from the Siwaliks was described as a new species, Sivapithecus aiyengari (Prasad, 1962).

The first Miocene hominoids from China were described as a new species, Dryopithecus keiyuanensis (Woo, 1957) based on an associated set of five lower cheek teeth. The species was referred to Dryopithecus on the basis of its resemblance, in size and morphology, to D.punjabicus. This species had been referred to Bramapithecus by Lewis (1937), so the Chinese material should not be considered to show any particular affinities with the western European Dryopithecus.

In the first of many papers discussing the phylogentic status of Ramapithecus, Simons (1961) argued that, since Leakey had pushed back the knowledge of hominids to the beginning of the Pleistocene and Ramapithecus was likely to be older than that, the R.brevirostris type palate could be defined as being within, or near, the population ancestral to the Pleistocene hominids. Simons (1961) regarded the jaws of Sivapithecus as being essentially similar to Dryopithecus.

(g) Revision of the later Miocene Hominoidea (Simons and Pilbeam, 1965) (Table 3.2)

In 1965 Simons and Pilbeam produced a preliminary revision of the Dryopithecinae in which all of the dryopithecines were referred to a single genus, Dryopithecus. More significantly three subgenera were recognised which fundamentally changed the taxonomy of later Miocene hominoids, particularly those from Indo-Pakistan (Table 3.2). The three groupings of Dryopithecines were an early Miocene African group, Dryopithecus (Proconsul), a Eurasian and African Middle Miocene group, Dryopithecus (Sivapithecus) and a predominatly European group, Dryopithecus (Dryopithecus). In addition they retained G.blacki as a valid species and genus, and Ramapithecus punjabicus was redefined (Table 3.2) and retained as a member of the Hominidae.

Most of the European Middle Miocene material was referred to D.fontani, including the Vienna Basin material referred to Sivapithecus by Lewis (1937). The Spanish taxa, H.laietanus and S.occidentalis (Villalta and Crusafont, 1944) were assigned to (Dryopithecus) laietanus as were two Siwalik specimens, a mandible (GSI D298) and an isolated tooth (YPM 13833).

The Sivapithecus indicus hypodigm of Lewis (1937), (Table 3.1) was expanded (Table 3.2) to include Lewis' (1937) S.giganteus hypodigm (and therefore Von Koenigswald's Indopithecus), S.aiyengari (Prasad, 1962); A.meteai from Turkey (Ozansoy, 1957), and part of the hypodigm of D.keiyuanensis (Woo, 1958). The (Sivapithecus) sivalensis hypodigm of Simons and Pilbeam (1965) (Table 3.2) slightly expanded that of

Table 3.2: Systematic revision of the later Miocene hominoids (Simons and Pilbeam, 1965).

Simons and Pilbeam (1965) taxa	Species to which the hypodigm had previously been assigned
Dryopithecus (D.) fontani (Lartet, 1856)	Dryopithecus fontani (Lartet, 1856)
	Paidopithex rhenanus (Pohlig, 1895)
	Dryopithe us rhenanus (Schlosser, 1901)
	D.darwini (Abel, 1902)
	D.germanicus (Abel, 1902)
	Austriacopithecus weinfurteri (Ehrenberg, 1938)
	Udabnopithecus garadziensis (Burtschah-Abramovitsch and Gaachuili, 1950)
D.(Dryopithecus) laietanus (Villalta and Crusafont, 1944)	Hispanopithecus laietanus (Villalta and Crusafont, 1944)
	Sivapithecus occidentalis (Villalta and Crusafont, 1944)
	Ramapithecus cf. brevirostris (Gregory et al., 1938)
D.(Sivapithecus) indicus (Pilgrim, 1910a)	Pithecus cf. satyrus (Falconer, 1868)
	* Sivapithecus indicus (Pilgrim, 1910a)
	* Dryopithecus frickae (Brown et al., 1924)
	* Sivapithecus himalayensis (Pilgrim, 1927)
	* S.orientalis (Pilgrim, 1927)
	* Dryopithecus sp. (Pilgrim, 1927)
	* Sivapithecus middlemissi (Pilgrim, 1927)
	Dryopithecus giganteus (Pilgrim, 1915)
	Indopithecus giganteus (von Koenigswald, 1949)
	Sivapithecus giganteus (Lewis, 1937)
	Ankarapithecus meteai (Ozansoy, 1957)
	Dryopithecus keiyuanensis (Woo, 1958, partim)
	Sivapithecus aiyengari (Prasad, 1962)
D.(Sivapithecus) sivalensis (Lydekker, 1879)	* Palaeopithecus sivalensis (Lydekker, 1879)
	* Dryopithecus chinjiensis (Pilgrim, 1915)
	* Palaeosimia rugosidens (Pilgrim, 1915)
	* P.(?) sylvaticus (Pilgrim, 1927)
	* Dryopithecus pilgrimi (Brown et al., 1924)
	* D.cautleyi (Brown et al., 1924)
	* Ramapithecus hariensis (Lewis, 1934)
	Sugrivapithecus salmontanus (Lewis, 1934)
	S.gregoryi (Lewis, 1936)
	Sivapithecus africanus (Le Gros Clark and Leakey, 1950)
Ramapithecus punjabicus (Pilgrim, 1910a)	Dryopithecus fontani (Branco, 1897, partim)
	D.punj bicus (Pilgrim, 1910a)
	Ramapithecus brevirostris (Lewis, 1934)
	Bramapithecus thorpei (Lewis, 1934)
	B.? sivalensis (Lewis, 1934)
	Dryopithecus keiyuanensis (Woo, 1957, partim)
	Keny pithecus wickeri (Leakey, 1962)

Note: Samples preceeded by * were treated in the same way by Simons and Pilbeam (1965) as they had been by Lewis (1937) (see Table 3.1).

Lewis (1937) (Table 3.1) to include both species of Sugrivapithecus (Lewis, 1934, 1936) and also S.africanus (Le Gros Clark and Leakey, 1950).

The hypodigms of Bramapithecus and Ramapithecus defined by Lewis (1937) (Table 3.1) were combined into a single species, Ramapithecus punjabicus, by Simons and Pilbeam (1965) (Table 3.2). As well as reducing Lewis' taxa to a single species, Simons and Pilbeam referred K.wickeri (Leakey, 1962), material from the Swabian Jura (Branco, 1897), and part of the hypodigm of D.keiyuanensis (Woo, 1957) to R.punjabicus.

This interpretation gained, and still enjoys widespread acceptance among palaeoanthropologists. The major contributions which it made were to recognise two species of (Dryopithecus) predominantly found in Europe but with one or two Siwalik examples, two species of (Sivapithecus) which were predominantly from Indo-Pakistan but were also found in China and Africa and Turkey, and a single species of middle Miocene hominid, Ramapithecus punjabicus, which was found in Indo-Pakistan, China, Germany, and Africa.

Simons and Pilbeam (1965) suggested that the pattern of morphology seen in Ramapithecus reflected a major shift in adaptive zone which they considered might be correlated with increased manual dexterity and incipient bipedalism. Simons (1961, 1964, 1968 etc) became the major advocate of the hominid status of Ramapithecus recognising a number of features of the masticatory complex which were apparently

shared with Australopithecus.

(h) Later Miocene Hominoidea (1965 - 1983)

Following the revision by Simons and Pilbeam (1965) the division into geographical regions is less useful as taxa were recognised extending across considerable geographical areas. From this time on the description and interpretation of material from one site influenced the interpretation of material from other areas, something which had occured rarely prior to 1965.

A fourth tooth from the Vienna Basin was described by Steininger (1967) with further detailed descriptions of the original three specimens. He assigned all of the specimens to D.fontani darwini, in accordance with the revision by Simons and Pilbeam (1965).

Leakey (1967, 1968) did not accept the synonymy of S.africanus with S.sivalensis nor the synonymy of K.wickeri with R.punjabicus proposed by Simons and Pilbeam (1965). Leakey retained K.wickeri as a valid taxon and transferred the hypodigm of S.africanus to Kenyapithecus as a species ancestral to K.wickeri, with the nomen K.africanus. Other assorted specimens were also referred to this taxon (Leakey, 1967, 1968). Pilbeam (1969) and Andrews (1971) formally synonymised Kenyapithecus with Ramapithecus, but referred the whole hypodigm of K.africanus to species of Proconsul (Andrews, 1978). There is no doubt that part of the reason for this was that specimens from Rusinga Island were considered to be too old to be assigned to Sivapithecus or

Ramapithecus. The dissatisfaction with Leakey's K.africanus taxon led to the whole taxon being assigned to Proconsul rather than its composition being reassessed. Andrews and Molleson (1979) recognised that the specimens originally described as S.africanus were morphologically distinct from the rest of the K.africanus hypodigm. They reassessed the provenance of the holotype (M 16649) and concluded that it could not have come from Rusinga Island. They were unable to demonstrate which site the specimen was derived from but noted that it showed the greatest affinities with several levels of Maboko Island. The only part of the originally described hypodigm of S.africanus whose provenance was definitely known is an isolated tooth which is from Maboko Island. As Maboko Island is Middle Miocene, several million years younger than Rusinga Island, this result tended to emphasise the distinctiveness of the original S.africanus hypodigm. The view that this material should not be referred to Proconsul (e.g. Madden, 1980) has since been widely accepted. Andrews et al. (1978) described Miocene hominoids from the Dam formation of Saudi Arabia which they considered to show closest resemblance to the African Miocene species, particularly to those specimens which had been described as S.africanus.

Pilbeam (1969) and Simons and Pilbeam (1965) had assigned the Fort Ternan material to R.punjabicus. Andrews (1971) described a mandible from Fort Ternan which showed that there was at least a specific distinction between these samples, he assigned the Fort Ternan sample to Ramapithecus wickeri. The dental arcades of Ramapithecus wickeri were reconstructed by Walker and Andrews (1973) and were shown to be

less hominid like than had been argued by Simons (1961). Andrews and Walker (1976) described all of the primates from Fort Ternan and recognised Proconsul africanus and Proconsul nyanzae as well as R.wickeri.

A new species of Siwalik hominoid, Gigantopithecus bilaspurensis (Simons and Chopra, 1969a), was described for a relatively complete mandible. The species was diagnosed by its very massive jaws, with the tooth rows set close together and by having canines which quickly wore down to the level of the cheek teeth (Simons and Chopra, 1969a, 1969b; Pilbeam, 1970). This material has subsequently been synonymised with giganteus (Pilgrim, 1915) taking the nomen Gigantopithecus giganteus, (Szalay and Delson, 1979). Pandey and Sastri (1968) described a new species, Sivapithecus lewisi, based on a jaw which they considered to be too large for S.indicus. Simons and Pilbeam (1971) reexamined the D.(Sivapithecus) indicus material and found that it was rather unlike D.(Dryopithecus) as had been previously suggested (Table 3.3) and in fact showed a number of resemblances to R.punjabicus.

New material and more critical analysis had demonstrated that the major groups of dryopithecines were more distinct than had been recognised by Simons and Pilbeam (1965). Proconsul and Sivapithecus were therefore reinstated as full genera (Andrews and Tekkaya, 1976; Pilbeam, 1976; Simons, 1976). These three authors recognised that certain species of Ramapithecus, Sivapithecus and Gigantopithecus shared a derived dental complex related to thick enamel. They all

recognised that these features probably indicated a shared adaptive complex related to dietary strategies but still considered that Ramapithecus remained the most likely candidate for human ancestry. Andrews and Takkaya (1976) proposed that three major groups of Eurasian later Miocene hominoids be recognised (Table 3.4). These equated with Dryopithecus, Sivapithecus and Ramapithecus.

In the course of a preliminary descriptions of major new finds of Siwalik hominoids Pilbeam et al. (1977) suggested that Ramapithecus, Sivapithecus and Gigantopithecus represented a natural group (Table 3.5). This view was also proposed by Andrews (1977) and Pickford (1977). Different relationships within this group were recognised (Table 3.5) but the major feature linking the taxa in the group was thick enamel. Simons (1977) agreed that Sivapithecus and Gigantopithecus shared some hominid-like features with Ramapithecus, but believed that these reflected parallel adaptations rather than a close phylogenetic relationship. However, the presence of these characters in Ramapithecus were still interpreted to indicate a close relationship between Ramapithecus and humans (Simons, 1977). Pilbeam et al. (1977) recognised at least five hominoids from the Siwaliks; S.indicus, R.punjabicus, G.bilaspurensis, cf.D.laietanus and S.sivalensis the last of which they felt might not be a justifiable grouping.

A complete mandible of a small hominoid from Candir, Turkey was designated the type of a new species Sivapithecus alpani (Tekkaya, 1974). Andrews and Tekkaya (1976) reviewed the "Ramapithecus"

Table 3.3: Dental characters of Sivapithecus which have been used to distinguish it from the European species of Dryopithecus.

Author	Characters of Sivapithecus, distinct from Dryopithecus
Pilgrim (1915)	Broad upper molars with high cusps and folded enamel.
Brown et al. (1924)	More rounded molar cusps.
Pilgrim (1927)	Broad lower molars, cylindrical canine.
Lewis (1934)	Robust jaws, molar and canine morphology (unspecified).
Lewis (1937)	Low molar crowns with blunt cusps and large basal bulges.
Gregroy et al. (1938)	High crowns with blunt swollen cusps, faint occlusal ridges, no cingula, hyper robust mandibles.
Villalta and Crusafont (1944)	Very folded molar enamel.
Le Gros Clark and Leakey (1950)	Enlarged premolars, lack of molar cingula.
Simons (1970)	High degree of interstitial wear.
Pilbeam (1971)	Large cusps restricting the occlusal fovea, basal bulge to molar crowns.
Simons (1976)	Thick enamel.
Pilbeam et al. (1977), Andrews (1977)	Thick enamel, lack of cingula, megadonty.

Note: The characters listed above are those which the authors used for the first time, or which they stressed as being of particular importance.

Table 3.4: Groupings of Eurasian later Miocene hominoids (Andrews and Tekkaya, 1976).

Group 1: The subgenus Dryopithecus of Simons and Pilbeam (1965)

Group 2: Comprised all of the D.(S.)indicus and some of the larger D.(S.)sivalensis specimens of Simons and Pilbeam (1965), with the addition of material assigned to D.macedoniensis, B.altipalatus, G.freybergi, S.lewisi, and A.meteai.

Group 3: Consisted of all of the material which Simons and Pilbeam (1965) assigned to R.punjabicus (including R.wickeri) with the addition of some of the smaller specimens of D.(S.)sivalensis (particularly those originally classified as Sugrivapithecus), and of S.alpani, and Rudapithecus hungaricus.

Note: Andrews and Tekkaya (1976) suggested that each of these three major groups would contain two species.

Table 3.5: The definitions of the "thick-enamelled" Miocene Hominoidea.

Author	Grouping	Taxa included	Diagnostic features
Andrews (1977)	Not named	Ramapithecus, Sivapithecus, Gigantopithecus.	Thick enamel, loss of cingula, large cusps, reduced cusp projection, reduced occlusal ridge definition, increased wear gradient, robust jaws, premolars and M1 increased relative to M3.
Pilbeam et al. (1977)	Ramapithecidae	Ramapithecinae, Sivapithecinae.	Thick enamel, megadonty.
Pilbeam et al. (1977)	Sivapithecinae	Sivapithecus, Bodvapithecus, Ankarapithecus, Ouranopithecus.	Sexually dimorphic canines.
Pilbeam et al. (1977)	Ramapithecinae	Ramapithecus, Gigantopithecus, Rudapithecus.	Small canines, with reduced sexual dimorphism, canine/premolar complex resembles A.afarensis.
Pickford (1977)	Sivapithecinae	Ramapithecus, Gigantopithecus, Sivapithecus.	Thick molar enamel, relatively flat interface between dentine and enamel, differential wear, facial shortening, small-bodied/large-toothed.

material in Kenya and Turkey and decided that S.alpani and R.wickeri (formerly K.wickeri) were conspecific and should be called R.wickeri. Andrews and Tobien (1977) described a large collection of isolated teeth of Miocene hominoids from Pasalar in Turkey. This collection can be divided into two size groups which Andrews and Tobien (1977) regarded as being too distinct to be the result of sexual dimorphism. The large form was assigned to Sivapithecus darwini and the small form to R.wickeri. Andrews and Tobien (1977) considered that Lewis (1937) had correctly referred the darwini material to Sivapithecus rather than to Dryopithecus fontani as had been suggested by Simons and Pilbeam (1965). They also believed that the similarity between the two size classes at Pasalar indicated either a close affinity between Ramapithecus and Sivapithecus, or that the Pasalar teeth represented a sample from an early stage in the radiation of these genera.

The mandible of a medium sized hominoid from the Miocene of Greece was described as a new species and genus, Graecopithecus freybergi (von Koenigswald, 1972). Further new material from Greece was described by de Bonis et al (1974, 1975; de Bonis and Melentis, 1976, 1977a, 1977b 1978). The material comprises one of the most complete collections of mandibles of any hominoid species from the later Miocene. The material was named Dryopithecus macedoniensis (de Bonis et al, 1974), but was later made the type species of a new genus, Ouranopithecus (de Bonis and Melentis, 1977a). Ouranopithecus macedoniensis was described as a very large hominoid with teeth rather similar in form to those of Australopithecus, Ramapithecus and Sivapithecus. A complete palate and partial lower face from the

Miocene of Turkey was described by Andrews and Tekkaya (1980). They suggested that the new material showed that Sivapithecus meteai was distinct from S.indicus (Simons and Pilbeam (1965) had synonymised these taxa). Andrews and Tekkaya (1980) noted that where differences were apparent between S.meteai and S.indicus, S.meteai showed what they interpreted as the derived condition and shared these features with O.macedoniensis. They therefore suggested that S.meteai and O.macedoniensis were conspecific and that the correct nomen for them was S.meteai.

An important collection of later Miocene hominoids from Rudabanya in Hungary was described as two new species and two new genera; Rudapithecus hungaricus (Kretzoi, 1969) and Bodvapithecus altipalatus (Kretzoi, 1975). R.hungaricus was diagnosed as being gracile with a short face, having a flat palate, a sub parabolic dental arcade, having a relatively small I^1 and low crowned molar teeth. B.altipalatus was diagnosed as a robust form, larger than Rudapithecus, with a high palate, relatively high crowned cheek teeth with marked cingula and a heavily sculptured surface to the thick enamel. Kretzoi (1975) considered Rudapithecus to be more advanced than R.brevirostris (he rejected the synonymy of this species with D.punjabicus) despite its older age. He concluded that Rudapithecus was directly ancestral to Man, passing through Pithecanthropus modjokertensis, with the australopithecines representing an extinct side branch which paralleled human evolution. The affinities of Bodvapithecus were not discussed.

Greenfield (1978, 1979) attacked the hominid status of Ramapithecus. He argued that in the known adaptive and morphological features the 'Ramapithecus' species are almost indistinguishable from those of contemporary Sivapithecus species. Greenfield (1979) argued that 'Ramapithecus' exhibits no more similarities to the Plio/Pleistocene hominids than does Sivapithecus, and that in fact Sivapithecus is more like A.afarensis than it is like the extant hominoids. Using Rudapithecus as an example of Ramapithecus he demonstrated that Ramapithecus and Sivapithecus overlap considerably. This is not too surprising, since he included the Holotype of R.punjabicus in his sample of Sivapithecus! Greenfield (1979) produced a revision of Sivapithecus which incorporated Ramapithecus (from Kenya and the Siwaliks) but he did not assign Rudapithecus to this genus although his synonomy argument rested on its identification as Ramapithecus!

A new species of Ramapithecus was described from the Miocene of China based on a relatively complete but crushed mandible. This was named Ramapithecus lufengensis (Lu et al., 1978). It was diagnosed by a parabolic dental arch, small and slightly bicuspid canine, completely bicuspid P_3 and molariform P_4. The authors considered that the dental arch shape distinguished this species from D.keiyuanensis and from Sivapithecus and concluded that, of the known species of Ramapithecus, R.lufengensis was the closest to humans. A second mandible from Lufeng was described as a new species, Sivapithecus yunnanensis (Xu and Lu, 1979), and was considered to resemble S.indicus. Xu and Lu (1979) suggested that S.yunnanensis is more like the orang-utan than any other know Neogene fossil hominoids and that

this species could be directly ancestral to Pongo pygmaeus. Subsequently large collections of specimens of both species have been recovered from Lufeng including skulls of both species (Lu et al, 1981; Wu et al, 1981; 1982). The skull of S.yunnanensis was suggested to show resemblances to both the orang-utan and to robust australopithecines (Lu et al, 1981). The skulls of R.lufengensis were interpreted as confirming its position near to the ancestry of man (Wu et al, 1981; 1982).

A large number of hominoid specimens have been recovered from Indo-Pakistan by expeditions under the direction of Professor David Pilbeam and Dr. S M Ibrahim Shah. These specimens were described by Pilbeam et al. (1980) and were interpreted as representing at least three species of hominoid, R.punjabicus, S.indicus and G.bilaspurensis. The majority of the hominoids come from sites being around eight million years old (Pilbeam et al., 1980). Pilbeam et al. (1980) considered these forms to be part of a family, Ramapithecidae (Table 3.5), defined largely by having thick occlusal enamel. Their postcranial skeletons were considered to show advances over dryopithecids and to more closely resemble extant great apes. More recently Pilbeam and Smith (1981) Pilbeam, (1982) and Preuss (1982) have described a partial skull of S.indicus (GSP 15000) which Andrews and Cronin (1982; Andrews, 1982), Preuss (1982) and Ward and Pilbeam (1983) have interpreted as showing shared derived specializations with the orang-utan. Lipson and Pilbeam (1982) and Ward and Pilbeam (1983) have recognised some of these features in the type maxilla of R.brevirostris. Andrews and Cronin (1982) and Martin and Andrews

(1982) have suggested that Ramapithecus should consequently be seen as a junior synonym of Sivapithecus.

Recently von Koenigswald (1981, 1983) and Dehm (1983) have described hominoids from Pakistan which were collected many years ago. von Koenigswald (1981) named a new species and genus, Chinjipithecus atavus, which he considered to be ancestral to Gigantopithecus. Although the type specimen is smaller, von Koenigswald believed that it closely resembled the type of giganteus (Pilgrim, 1915). von Koenigswald (1981) assigned giganteus, including bilaspurensis, to Gigantopithecus, as G.giganteus. If he has maintained his earlier position (von Koenigswald, 1949) he could have assigned the new species to Indopithecus but as he had recognised Indopithecus as a junior synonym of Gigantopithecus he felt that a new genus was necessary.

Material discovered at Moroto, Uganda, was referred to Proconsul major by Allbrook and Bishop (1963) and Pilbeam (1969). This attribution was made on the basis of size as no complete maxillary material was available from Songhor for comparison. Recently new Proconsul major material from Koru, the type site, has been described (Martin, 1981). This material included an associated maxillary postcanine tooth row which is quite different to that from Moroto (Martin, 1981). It is possible that the Moroto hominoid material falls within the limits of later Miocene hominoids. Pickford (1982) has recently described new hominoid material from the middle Miocene beds at Majiwa and Kaloma, which correspond with the nearby Maboko

Island deposits. Pickford believes that Kenyapithecus is a valid genus which includes material from Maboko and from Fort Ternan. He suggests that a smaller ramapithecine, equal in size to R.punjabicus, is also present at Kaloma, Majiwa and Maboko, but not at Fort Ternan. Pickford (1982) also reports the presence of a dryopithecine at Majiwa, which he considers resembles a molar from Fort Ternan, others from Moruorot and the Moroto palate.

Kay (1982b) has recently described a new species, Sivapithecus simonsi, from Indo-Pakistan based on a mandible, GSI D 298, which has been lost. The hypodigm for this species is the Siwalik material which Simons and Pilbeam (1965) assigned to D.laietanus with the tentative addition of GSI D-185.

The most recent revision of the later Miocene hominoids is that by Kay and Simons (1983; Kay, 1982b). This concentrated on Sivapithecus (including "Ramapithecus"). Kay and Simons (1983) recognised five named species and suggested that two further species were indicated. S.indicus was recognised for the larger specimens in the Siwalik sample, including S.lewisi, broadly similar to D.(S)indicus of Simons and Pilbeam (1965) but with important additions. Kay and Simons (1983) assigned to S.indicus the Chinese specimens described by Woo (1958), as had Simons and Pilbeam (1965), and also the hypodigms of S.yunnanensis, B.altipalatus, S.meteai, G.freybergi, the smaller specimens described as O.macedoniensis and probably the large teeth from Pasalar referred to S.darwini by Andrews and Tobien (1977). The smaller specimens from the Siwaliks, including "Ramapithecus", were

assigned to S.sivalensis. To this species Kay and Simons (1983) also referred the hypodigm of R.lufengensis and the type series of D.keiyuanensis (Woo, 1957), they also provisionally referred S.alpani to this species (the holotype only). The Siwalik material which Simons and Pilbeam (1965) had referred to D.laietanus was assigned to Sivapithecus as Kay (1982b) believed that photographs of GSI D-298 showed that this specimen had thick enamel! This material was not considered compatible with any other Siwalik species and Kay (1982b) named a new species for it, S.simonsi. The largest specimens from the Siwaliks were regarded as distinct from Sivapithecus by Kay and Simons (1983) and was recognised as G.giganteus. Kay and Simons (1983) recognised S.darwini for the Vienna Basin material, but felt that the large Pasalar teeth assigned to this taxon by Andrews and Tobien (1977) was more similar in size to S.indicus. The small specimens from Pasalar were suggested to represent an unnamed species of Sivapithecus which might also be represented in Pakistan. The large specimens of O.macedoniensis were suggested to represent a second new species of Sivapithecus. Finally, Kay and Simons (1983) assigned all of the Kenyan material which had previously been called R.wickeri or S.africanus to S.africanus. The Rudapithecus material from Rudabanya which Simons (1976) had previously recognised as Ramapithecus was considered to be D.fontani by Kay and Simons (1983).

This revision defined species groupings on the basis of size, although this resulted in S.indicus containing specimens whose facial morphology is quite distinct, e.g. the Rudabanya (B.altipalatus) frontal and GSP 15000. The only species which were not defined by

tooth size were the medium or small species, S.sivalensis and S.africanus and Kay and Simons (1983) specifically state that geographical and temporal factors influenced this decision. Other workers continue to recognise a large number of genera for the Sivapithecus hypodigm as defined by Kay and Simons (1983). One of the characters which links the species of Sivapithecus (in the sense of Kay and Simons, 1983) is thick molar enamel. This they interpret as a character unique to man's family. This assumption has the consequence that all samples which appear to have thick enamel must be hominids and are therefore crammed into a single genus. This assumption is evaluated in Chapters 4, 5 and 6. For the present it cannot be assumed to be valid.

(i) Discussion of the literature

The similarity between Sivapithecus and Ramapithecus which was increasingly recognised during the late 1970s has resulted in almost all workers placing both of these genera in Sivapithecus. Some workers prefer to exclude the African species from this genus (Pickford, 1982) and others retain Ouranopithecus as a genus. Views regarding the relationships of Sivapithecus have polarised. One group of workers, Ward, Pilbeam, Andrews, see Sivapithecus as being part of the orang-utan clade, while Kay and Simons (1983; Kay, 1982b) see Sivapithecus as being part of the human clade. Many other interpretations for the ancestry of extent great apes have previously been proposed (Table 3.6). The case for Sivapithecus being an early hominid stands and falls on the interpretation of thick enamel as

being a hominid character.

Kay and Simons (1983) recognised three genera of later Miocene hominoids, Sivapithecus, Gigantopithecus and Dryopithecus, but have only attempted to address the relationships of one of these, Sivapithecus. Others (e.g. Pickford, 1982; Ward and Pilbeam, 1983) would recognise at least four genera, adding Ouranopithecus, and possibly five, adding Kenyapithecus. Attention has been focused on the successor to Ramapithecus; Sivapithecus, while few attempts have been made to define the place of Dryopithecus, Gigantopithecus or Kenyapithecus, or even Ouranopithecus in the evolution of Hominoidea. One of the fundamental reasons for this is that the significance of cheek teeth with thick enamel, which appears to be characteristic of all of the later Miocene hominoids except for Dryopithecus is unknown. That question is addressed in the light of metrical data (a novel approach!) in the following chapters of this thesis. The composition of species groupings is independent of these data although the combination into genera does depend on it to some extent. The differences in opinion between Kay and Simons (1983) and others (Martin and Andrews, 1982; de Bonis, 1983; Ward and Pilbeam, 1983) as to the constitution of for example S.indicus mean that only personal observations of the original material can be used with any confidence to discuss relationships between taxa.

Table 3.6: The proposed ancestors of modern hominoids.

	Homo	Pan	Gorilla	Pongo
Lartet (1856)	D.fontani **			
Lydekker (1879)		P.sivalensis **		
Lydekker (1886)		T.sivalensis ***		
Pilgrim (1910b)		A.sivalensis ***		
Pilgrim (1915)	S.indicus **			
Remane (1921)				Palaeopithecus ***
Remane (1921)				D.giganteus ***
Gregory (1922)				Sivapithecus **
Pilgrim (1927)			D.chinjiensis **	
Lewis (1934)	Ramapithecus *			
Lewis (1934)	Bramapithecus *			
von Koenigswald (1935)	G.blacki *			
Gregory et al.(1938)	Ramapithecus *			Sivapithecus **
Gregory et al.(1938)	Bramapithecus *			
Simons (1961)	R.brevirostris **			
Leakey (1962)	K.wickeri **			
Simons and Pilbeam (1965)	Ramapithecus **			
Pilbeam (1969)		D.africanus **	D.major **	
Andrews (1971)	Ramapithecus **			
Conroy (1972)	Ramapithecus **			
Frayer (1973)	Gigantopithecus **			
Eckhart (1975)	Gigantopithecus **			
Kretzoi (1975)	Rudapithecus **			
Andrews (1976)	Ramapithecus *			
Pilbeam (1976)	Ramapithecus *			
Simons (1976)	Ramapithecus *			
Gantt et al. (1977)	Ramapithecus **			
Xu and Lu (1979)	R.lufengensis *			S.yunnanensis **
Andrews and Tekkaya (1980)				S.meteai *
Andrews and Cronin (1982)				Sivapithecus *
Ward and Pilbeam (1983)				Sivapithecus *
Kay (1982b)	Sivapithecus **			
Kay and Simons (1983)	Sivapithecus **			

Notes: These authors interpretations of the fossil species are symbolised as follows:

* = Probably represents an ancestral population from which modern is derived.

** = Directly ancestral to modern genus.

*** = Congeneric with modern form.

II. SPECIES GROUPINGS OF LATER MIOCENE HOMINOIDEA

1. Introduction

The principles of zoological taxonomy require that specimens be assigned to taxonomic units on the basis of similarity to a particular specimen, which has previously been designated the holotype for a species. This method often cannot be used in palaeontology as several species are based on holotypes which are postcranial elements (e.g. Austriacopithecus weinfurteri) which means that cranio-dental specimens can only be compared to the holotype on the basis of size. A number of taxa of later Miocene hominoids are based on type specimens which are isolated teeth and no type specimen comprises a whole dentition. Only teeth which are also present in the holotype can be assigned to a particular species if the rules of zoological taxonomy are strictly followed. This problem is the result of the use of incomplete specimens as holotypes, but is difficult to avoid as fossil taxa must be named to facilitate communication and it would be impractical, and unrealistic, to await the discovery of a complete specimen to use as holotype. A common way around this problem is to use the most complete specimens known at any one time to group less complete specimens together. However, this method tends to place the most complete specimen centrally in the variation of the species, which may not be justified. The procedure for zoological taxonomy was designed for extant forms where a complete, and typical, example of the species could be selected as the holotype. It was not designed to cope with the problems of the fossil record and consequently requires modification for use in palaeontology.

A variety of procedures are employed by palaeontologists to establish species groupings of fossils. The approach which I have used involves the establishment of phena, the grouping of phena into phenon dentitions, and finally the grouping of phenon dentitions into palaeospecies. Phena are groupings of specimens of nearly identical size and morphology. Only homolous parts can be grouped in this way so phena were established for each tooth separately. This approach places no more emphasis on one specimen than any other. Phena for each tooth type are grouped into phenon dentitions by the use of complete specimens as all of the teeth in a single jaw must necessarily belong to one species. When associated upper and lower dentitions were not available then upper and lower teeth were assigned to phenon dentitions on the basis of occlusion. A number of later Miocene hominoid samples of similar morphology span a size range which is too large for a single species (see Chapter 2). In such cases phena were separated into size categories which were compatible with the variance in extant hominoids. When samples comprised only isolated dental specimens the size groups of each phena were assembled into species groupings on the basis of size. Phenon dentitions were compared to one anther to establish whether their morphology was compatible with both phenon dentitions belonging to a single species and if this was the case the variance in extant hominoids (Chapter 2) was used to assess whether the samples were metrically compatible. The species groupings of later Miocene hominoids established by this method are described below.

2. Sivapithecus

The Siwalik sample of first molars, upper and lower, is too variable to be accomodated in a single species when compared to living hominoid variance (Tables 2.3, 2.5, and 2.7). On bivariate plots most of the cheek teeth form two clusters, here recognised as S.sivalensis and S.punjabicus. S.punjabicus is morphologically indisinguishable from S.sivalensis in dentition and is recognised purely on metric grounds. Siwalik I^1s are too variable in size to represent a single species. The large specimens cluster with GSP-15000 and are consequently assigned to S.sivalensis. The smallest specimens are assigned to S.punjabicus, purely on the basis of size. An intermediate size group of I^1s could be linked with either species on metrical grounds and cannot therefore be assigned. Based on my own observation of the original material the Siwalik Sivapithecus sivalensis seems to be more similar to Siwalik S.punjabicus specimens than it is to specimens from other sites. For this reason I have rejected Kay's (1982b) broader definitions of these hypodigms.

(a) Sivapithecus sivalensis (Lydekker, 1879)

Holotype: GSI D-1 parts of a maxilla with C^1, P^4 - M^3.

Referred material:

Associated specimens; GSI D-177. -189, -191, -196, -197, -198,

GSI D-299/300, -18039, -18040, -18064;

GSP-4230, -4735, -9564, -9895, -9977, -11704, -11707, -11708, -11786,

GSP-13165, -13566, -15000, -15557, -16075.

YPM-13828, -13837.

AMNH-19413.

ONGC V-790.

BSPhG-1939 X 2.

Isolated teeth:

I^1: GSP-3293, YPM-16919.

I^2: GSP-9901.

C^1: GSP-10232. -10493, -11003, -12568, -13167, -13622,

GSP-14997; GSI D-192, -238, -307, -308, -18066; YPM-13809; M-34483.

P^4: GSP-9987, -13166; GSI D-18065.

M^1: GSP-5260, -6206; GSI D-301; YPM-13834; M-13365, -13366.

M^2: GSP-9969, -9972, -9986, -10500, -11999; GSI D-302; YPM-13835;

BSPhG-1939 X 3.

M^3: GSI D-188, -309; YPM-13827.

I_1: GSP-5464, -12648, -13164.

C_1: GSP-8679, -8925, -9905; BSPhG-1939 X 599.

P_3: GSI D-190.

M_1: GSI D-178, -18041.

M_2: GSP-5001, -7144, -11998, -15255; GSI D-176; YPM-13832.

M_3: GSP-13162, -S214; GSI D-179, -303; M-13364.

Synonyms:

Palaeopithecus sivalensis (Lydekker, 1879)

Sivapithecus indicus (Pilgrim, 1910a)

Sivapithecus orientalis (Pilgrim, 1927)

Sivapithecus himalayensis (Pilgrim, 1927)

Sivapithecus middlemissi (Pilgrim, 1927)

Sivapithecus aiyengari (Prasad, 1962)

Dryopithecus (?) frickae (Brown et al., 1924)

Sivapithecus lewisi (Pandey and Sastri, 1968)

Palaeosimia rugosidens (Pilgrim, 1915)

Dryopithecus chinjiensis (Pilgrim, 1915)

Sivapithecus sivalensis is the type species of Sivapithecus, by synonymy with S.indicus and priority of naming. Palaeopithecus is not available as a generic name for hominoids (Lewis, 1937). The hypodigm recognised here is what is usually known as Sivapithecus indicus, but with some additions. In terms of canine, P^4, M^1 the holotype cannot be separated from the usually recognised hypodigm of S.indicus. Only in M^3, which is small in the holotype, could any distinction be drawn, and there are no significant differences in this tooth on the basis of extant hominoid variation (Chapter 2). A few specimens could be identified as regards sex. GSI D-196 and GSP-15000

are both males (C^1/M^1 1.44 and 1.39 respectively, see Table 2.9), GSI D-299/300 is a female (C^1/M^1 = 1.00, see Table 2.9). The premolars and molars of D-299/300 cluster with the S.sivalensis hypodigm on length/breadth plots, although the canine of D-299/300 is the smallest known from the Siwaliks. The largest C^1 is M-34483, and a comparison of the maximum length of these two specimens gives an index of 1.66, which is within the limits of this index in living hominoids (Table 2.7). On this basis all of Siwalik C^1s were assigned to S.sivalensis as none can be shown to represent the smaller species. This undoubtedly means that some isolated C^1s of S.punjabicus have been assigned to S.sivalensis, but metrically there is no reason to assign all known upper canines to more than one species, S.sivalensis. If the canines of S.punjabicus are found in association with postcanine teeth this would facilitate the sorting of canines into species with more precision. Until such time the assumption that C^1s are sampled from both sexes of both species (Kay, 1982a, 1982b) cannot be justified.

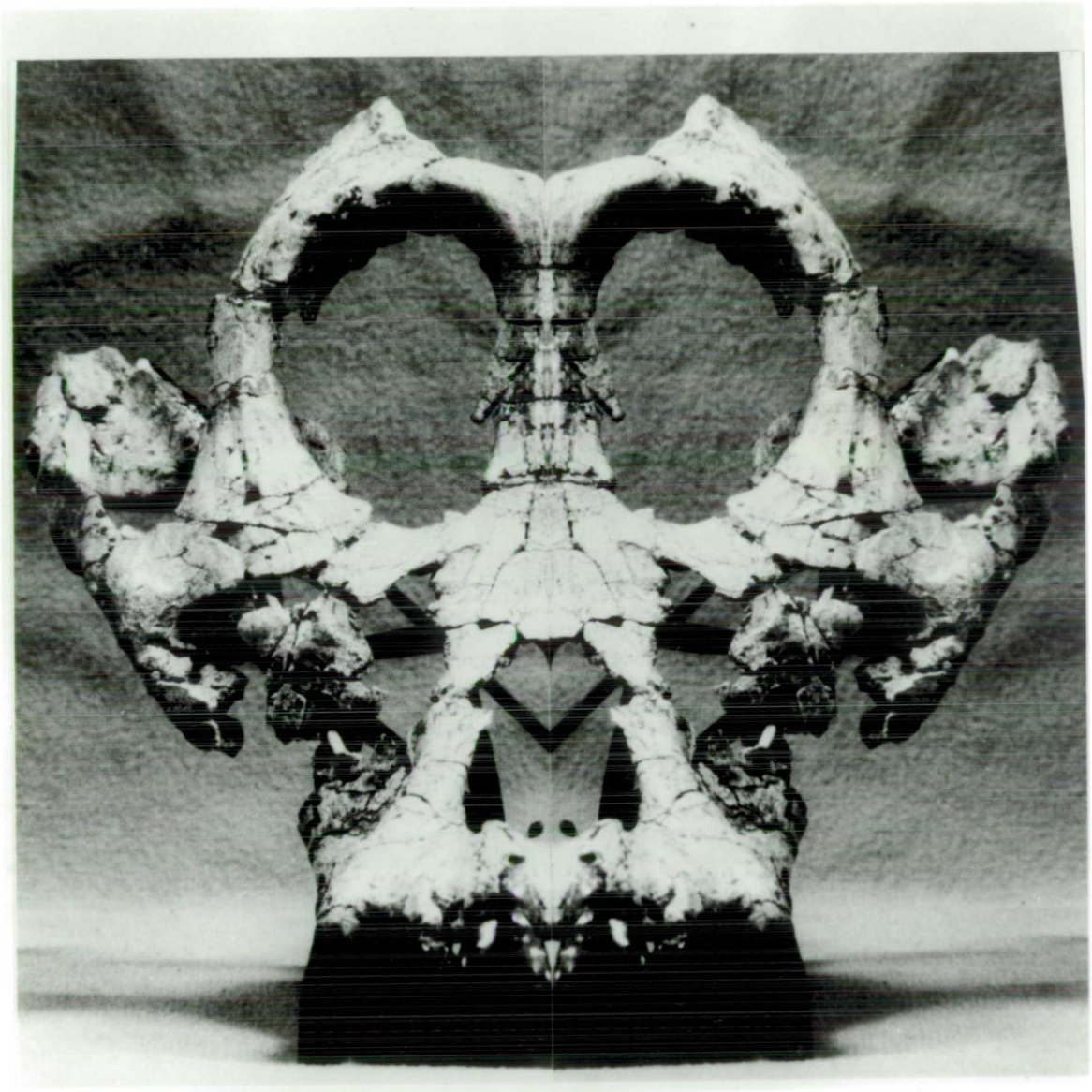
In all cases the teeth assigned to S.sivalensis form a hypodigm which is metrically justifiable on the basis of the data presented in Chapter 2 (Tables 2.5 and 2.7). A few specimens fall beyond the cluster for the S.sivalensis hypodigm on length/breadth plots, although these can all be reasonably included in the species on the basis of living hominoid variance (Tables 2.5 and 2.7). All of these specimens are larger than is typical for S.sivalensis, and more complete material may show them to be specifically distinct from S.sivalensis. These are GSID-190, ONGG V-790, and undescribed

material in the collections of Profs. Dehm and von Koenigswald. In all teeth S.sivalensis is distinguished from S.punjabicus by its greater size, though some overlap in the ranges of dental dimensions does occur, in M_3, P_4, M^3, Overlap may occur in other tooth types but this cannot presently be demonstrated. This inevitably means that some isolated specimens, which have been assigned to a species on the basis of size will have been misidentified.

Sivapithecus sivalensis is exemplified by the recently described partial skull, GSP-15000 (Figure 3.1) (Pilbeam and Smith, 1981; Pilbeam, 1982; Preuss, 1982). The morphology has been thoroughly described elsewhere, but important additions to these descriptions arising from my work are the facts that S.sivalensis has thick enamel and relatively flat dentine horns (see Chapter 4). The wear pattern in which cheek teeth wear nearly flat before the enamel is perforated through to the dentine (dentine fusion wear, see Chapter 4) is typical for this species. Also diagnostic for this species is the robusticity of the mandibular corpora. A more detailed listing of the derived features defining this species is made in Chapter 6, (Figure 6.5).

Figure 3.1: Photographic reconstruction of the face of Sivapithecus sivalensis (CSP-15000).

The reconstruction was made by printing a reversed copy of the negative showing the existing left side of the face. The two photographs were alligned with the central incisors making contact and with homologous points in the region of the nasal bones overlapped. The reconstruction provides little new information, but facilitates comparison with complete modern material. The narrow septum between the orbits is more clearly seen than in the original half face. The derived characters which S.sivalensis shares with Pongo are listed in Figure 6.5.



(b) Sivapithecus punjabicus (Pilgrim, 1910a)

Lectotype: GSI D-118/119 part of left and right mandibles with M_2 and M_3.

Referred material:

Associated specimens:

GSI D-185, -199; GSP-4622, -6153, -6160, -7619, -9563, -13445, GSP-15556, -16077; YPM-13799, -13806, -13807, -13811, -13814, -13825; AMNH-19411, -19412.

Isolated specimens:

I^1: GSP-8928, -9903, -13558, -13931.

P^4: GSP-9906.

M^1: GSP-5019, -8836, -13810; GSI D-187.

M^2: GSP-7308, -7618, -9896; GSI D-313; BSPhG-1939 X 1.

M^3: GSP-5067, -6758, -8702, -9900, -13460; GSI D-186, -18068.

C_1: ? GSP-13622

P_4: GSP-5020; GSI D-18069.

M_1: GSI D-180, -181, -304, -305, -306; YPM-13813.

M_2: GSP-4635; GSI D-18042; C.atavus holotype.

M_3: GSP-6759. -8926, -8927, -9899, -9930, -10785, -13700, -15030; GSI D-314, -180067; YPM-13833, -13836; M-13264, -13367.

Synonyms:

Dryopithecus punjabicus (Pilgrim, 1910a)

Palaeopithecus (?) sylvaticus (Pilgrim, 1927)

Ramapithecus brevirostris (Lewis, 1934)

Dryopithecus sivalensis (Lewis, 1934)

Ramapithecus hariensis (Lewis, 1934)

Sugrivapithecus salmontanus (Lewis, 1934)

Bramapithecus thorpei (Lewis, 1934)

Sugrivapithecus gregoryi (Lewis, 1936)

Dryopithecus pilgrimi (Brown et al., 1924)

Dryopithecus cautleyi (Brown et al., 1924)

Chinjipithecus atavus (von Koenigswald, 1981)

No specimens could be reliably identified as regards sex, using the indices in Table 2.9. On the basis of morphology and size, it seems likely that AMNH-19412 is a male, and YPM 13811 a female.

Sivapithecus punjabicus, as recognised here, corresponds with Ramapithecus punjabicus of Simons and Pilbeam (1965) with some additions. It corresponds with the hypodigm which Kay (1982b) called S.sivalensis except that it is only recognised for specimens from Indo-Pakistan.

Unassigned Siwalik material:

I^1: GSP-6999, -9898, -13171, -13930.

This material could be assigned to either S.sivalensis or to S.punjabicus on the basis of size. It has not been assigned because more detailed study, which Jay Kelley is presently undertaking, may resolve their attribution more precisely than metrical methods.

(c) Sivapithecus meteai (Ozansoy, 1957)

Holotype: MTA mandible with I_2 - M_3

Referred material: MTA-2125; RPL-54, -55, -56, -75, -76, -85, RPL-128, -197, -199, -208, -209, -391; Erlangen mandible.

Synonymies:

Ankarapithecus meteai (Ozansoy, 1957)
Graecopithecus freybergi (von Koenigswald, 1972)
Dryopithecus macedoniensis (de Bonis et al., 1974)
Ouranopithecus macedoniensis (de Bonis and Melentis, 1977a)
Sivapithecus unnamed species B (Kay and Simons, 1983)

Two of the mandibles of S.meteai can be identified as females, RPL-54 and RPL-197 (C_1/M_1 0.84 and 0.81 respectively, see Table 2.9). In addition RPL-55 and RPL-56 are possibly females (C_1/M_1 0.92 and 0.94 respectively, see Table 2.9). No males can be reliably identified, and the maxilla RPL-128 can only be said to be likely to be a female (C^1/M^1 1.11, see Table 2.9).

The teeth which are best represented are M_2 and M_1 respectively. Kay and Simons (1983; Kay, 1982b) have recently suggested that the Rain Ravine material could not represent a single species. For M_1 the coefficient of variation is too high for a single species (my data), but only five specimens are represented. When the largest (RPL-75) and the smallest M_1s (RPL-54) are compared these give a maximum/minimum length index length of 1.23, which is within the

limits of modern hominoids (Table 2.7). Similarly the range expressed as a percentage of the mean gives a value of 0.21 which is within the variance of modern hominoids (Table 2.5). For C_1 maximum length the CV is 13.25 for 7 Rain Ravine specimens which is within the range for living hominoids (Table 2.3). Both the index of max/min and of range expressed as a percentage of the mean for C_1 maximum length result in values (1.48 and 0.39, respectively) which are within the limits for extant great apes (Tables 2.5 and 2.7). Consequently there seems no good reason to recognise two species among the morphologically homogeneous sample from Rain Ravine. The reason why Kay and Simons (1983) did so was because they used an inappropriate method of variance analysis for such a small sample.

The Macedonian material strongly resembles the very heavily worn Pygros mandible, housed at the Geologisches Institut, Erlangen (but currently on loan to the author at BMNH for reconstruction). It was described by von Koenigswald (1982). The M_1 is smaller than those of Rain Ravine and cannot be fitted into that hypodigm using any of the variance analyses described in Chapter 2. However, a remarkable degree of interstitial wear appears to have reduced the length of the tooth by about 25%. A 25% increase in M-D length would place the specimen within the range found in Rain Ravine specimens. The P_4 in the Pygros mandible is much less worn than is the M_1 (which has deep concavities mesially and distally). The P_4 in the Pygros mandible is slightly smaller than RPL-197 but when added to the Rain Ravine P_4s the CV for the whole sample is 9.28 (n = 8) which is within the range of values found in extant hominoids (Table 2.3). For the same

samples the max/min index is 1.29, and the range expressed as a precentage of the mean is 0.26, both values being well within the variance of extant hominoids (Tables 2.5 and 2.7). The M_2 in the Pygros mandible is also reduced by interstitial wear and is somewhat smaller than the smallest Rain Ravine specimen. When the Rain Ravine and Pygros samples are combined for M_2 length they have a CV of 8.43 (n = 8) which is only just outside the values for extant hominoid species (Table 2.3). When the largest Rain Ravine M_2 (RPL-75) is compared to the Pygros M_2 the max/min index is 1.28, within the values for Pongo and Gorilla (Table 2.7) and the range expressed as a percentage of the mean is 0.25, which is compatible with extant hominoid variance (Table 2.5). On the basis of these data it is clear that the Rain Ravine sample cannot be separated, even taking measurements on heavily worn teeth, from the Pygros mandible, either on metrical or morphological grounds.

The type mandible of S.meteai has teeth which fall within the range of variation of the Rain Ravine sample for every tooth. There can be no metrical reason to separate these samples. The slightly different morphology of P_3 in the meteai type might justify the recognition of two species (Andrews, personal communication) but is not adopted here. If two species were to be recognised, the greek sample would take the species name freybergi If the Greek material is later found to be generically distinct from Sivapithecus, then it would take the name Graecopithecus.

Andrews and Tekkaya (1980) referred the Sinap palate, MTA-2125, to S.meteai. The C^1 of MTA-2125 is within the range of the Rain Ravine

sample. This combined sample is consistent with the variance in extant hominoids, max/min = 1.42 (see Table 2.7), range expressed as a percentage of the mean is 0.33 (see Table 2.5). The molars in MTA-2125 are somewhat smaller than the two Rain Ravine specimens. These samples are too small to use CV but the maximum M^1 breadth (RPL-128)/minimum breadth (MTA-2125) is 1.08, the range expressed as a percentage of the mean is 0.077, both values are within the variance of modern hominoids (see Tables 2.5 and 2.7). In addition the observed range of M^1 breadth for S.meteai (as defined here) is contained within the range for Gorilla and for Pongo. Similar results for M^2 breadth were also obtained.

There are therefore no good metrical or morphological grounds presently known which challenge the interpretation of the Turkish (Sinap) material and the Greek (Pygros and Rain Ravine) material as a single species, S.meteai. This species has very similar dental morphology to that seen in S.sivalensis and S.punjabicus. The anterior teeth are of similar size to those of S.sivalensis, although upper canines are broader and may extend beyond the range of S.sivalensis. Cheek tooth size is greater in S.meteai than in S.sivalensis, but the smallest Macedonian specimens (females) may overlap the upper end of the S.sivalensis range. The mandible of S.meteai is more gracile than in the Siwalik Sivapithecus, and P_3 has a very broad distal fovea. No metrical data are available for enamel thickness in S.meteai, but the molars wear with dentine fusion (see Chapter 4) and worn teeth suggest that the enamel in this species is thick. Ward et al. (1983) suggest that RPL-128 shows the Asian

subnasal morphology as does MTA-2125 (Andrews and Cronin, 1982).

(d) Sivapithecus darwini (Abel, 1902)

Holotype: Unnumbered M_3 in the collection of the Geological Society of Vienna.

Referred material:

I^1: BP-28, -1271, -1296, -1300

P^3: BP-43, -1302

P^4: BP-41, -42, -44, -45, -46, -74, -79, -1311

M^1: BP-33, -36

M^2: BP-29, -30, -32, -34, -35, -37; NHMW-14?

M^3: BP-20, -21, -22, -23, -24; NHMW-14?

I_1: BP-1303

C_1: BP-55, -56, -57, -58, -59

P_3: BP-50, -411, -1304, -1305, -1306

P_4: BP-49, -51, -52, -53, -1307

M_1: BP-5, -61, -62, -65, -68, -70, -71, -73, -1308

M_2: BP-60, -63, -64, -66, -67, -78

M_3: BP-1, -2, -3, -4, -6, -7, -15. Unnumbered specimen in the collection of the Institute of Paleontology, Univ. Vienna.

No type specimens of species other than the senior synonym have been assigned to this taxon. The sample of dental remains from Pasalar form a morphologically homogeneous sample. The largest number of teeth for this sample is for M_1. The CV for this sample is 8.90 for M_1 length (n = 12), which is greater than is usually found in one

species of hominoid (Table 2.2). The range expressed as a percentage of the mean gives a value of 0.25 which is higher than that found in any hominoid, with the exception of Pan paniscus, (see Table 2.5). The max/min index for M_1 length is 1.29 (BP-62/BP-1298) which is greater than is found in any living species (see Table 2.7). Two species were therefore recognised from Pasalar, and specimens were allocated according to size. When there were two distinct size categories with a small number of specimens somewhat intermediate, the intermediate group was assigned to a species such that the resulting variance (as measured in Chapter 2) was kept at a minimum for that species (i.e. if the intermediate group added to the darwini sample gave a max/min of 1.20 and the intermediate group added to the small species gave a max/min value of 1.15, the intermediate category was assigned to the small species). This approach is arbitrary, but is the best available until more complete material is recovered. When only one size category of a tooth was found (e.g. C_1) then this was assigned to a species by comparision to the size of M^1.

Sivapithecus darwini is distinguished from the Sivapithecus species described above by the retention of cingula on its molar teeth. It has thick enamel, and appears to have relatively flat dentine horns (see Chapter 4). Dental wear invariably proceeds in the manner described as dentine fusion (Chapter 4), inappropriately, but commonly, known as "thick-enamelled" wear.

(e) Sivapithecus alpani (Tekkaya, 1974)

Holotype: MTA-2253, mandible with P_3 - M_3.

Referred material:

I^1: BP-27, -1299

P^4: BP-48

M^1: BP-40 (see Griphopithecus suessi discussion below)

M^2: BP-19, -39

M^3: BP-25, -26

P_4: BP-54, -1297

M_1: BP-14, -1298

M_2: BP-13, -17, -69, -72

M_3: BP-8, -9, -10, -11, -12

No holotypes of other taxa have been assigned to this species. The change in name from Andrews and Tobien (1977), who assigned the material to R.wickeri, results from the separation of the Kenyan and the Turkish hypodigms. The hypodigm from Pasalar is consistent with the Candir mandible in terms of morphology and in size, although the Candir mandible represents one of the smaller known examples of S.alpani in dental dimensions. S.alpani has thick enamel on its molar teeth (Chapter 4) and has relatively flat dentine horns. Molar cingula are present to a greater degree than in S.sivalensis, S.punjabicus and S.meteai. As with all Sivapithecus the pattern of wear is the dentine fusion type (Chapter 4) commonly known as the "thick-enamelled" type.

(f) Discussion

The species darwini and alpani are provisionally referred to Sivapithecus on the basis of their resemblance to the Asian species in having relatively flat dentine horns. More complete material may later require generic separation of these forms if facial features differ significantly from the specialised condition seen in S.sivalensis, S.punjabicus and S.meteai.

The genus and species Griphopithecus suessi (Abel, 1902) was retained for the type specimen (NHMW-15) an M^1. This specimen has been incorrectly identified as a dp^4 (Abel, 1931). The specimen is heavily worn but shows dentine fusion wear ("thick-enamelled") something which is not seen in the deciduous teeth from Pasalar or from the Siwaliks. The crown of NHMW-15 appears low, which has led workers to interpret it as a deciduous tooth. In fact most of the lateral and cervical enamel has been lost by breakage, and where portions of the lateral enamel remain it is clear that the crown was as high as in permanent Sivapithecus molars. The type, and only specimen, of G.suessi cannot therefore by synonymised with S.darwini. It is morphologically similar to the Pasalar sample and metrically almost identical to the M^1 of S.alpani (BP-40). If these samples were combined then the genus Sivapithecus would become a junior synonym of Griphopithecus. This synonymy is not warranted on the basis of the present evidence as it would cause considerable confusion and the morphology of G.suessi is not sufficiently known to be certain of its generic affinities. If new finds of G.suessi, S.alpani and

S.darwini show that these species warrant separate generic status from Sivapithecus then the genus Griphopithecus is available. In the absence of such evidence and with the indication that S.alpani and S.darwini share a flat dentine surface with S.sivalensis and S.punjabicus these species were provisionally assigned to Sivapithecus, and G.suessi was recognised for the single specimen which cannot be assigned to Sivapithecus without major nomenclatorial changes.

3. Kenyapithecus

(a) Kenyapithecus africanus (Le Gros Clark and Leakey, 1950)

Holotype: M 16649, Maxilla with P^3 - M^1

Synonyms:

Kenyapithecus wickeri, Leakey, 1962

Referred material: KNM FT-7, -8, -34, -40, -45, -46, -47, -48, KNM FT-3318, -3636; KNM MJ-1, -2, -4, -5, -6; KNM MB-108; M-36370

Provisionally referred material: KNM FT-28, -39, -49, -2751; KNM MB-104

This species is what has previously been known as Ramapithecus wickeri (e.g. Andrews and Walker, 1976) with the addition of the holotype of S.africanus, and some Maboko and Fort Ternan material previously recognised as P.nyanzae (Andrews, 1978) and of recently described material from Majiwa and Kaloma (Pickford, 1982). Other Maboko specimens may also belong to this species (Harrison, personal communication). The only specimen which can be reliably sexed is the type of K.wickeri (KNM FT-46) which has a C^1/M^1 index of 0.88 and is therefore almost certainly a female (see Table 2.9). Thick enamel is not a useful criterion for the attribution of hominoid species to genera as thick enamel has either evolved in parallel in the Pongo and the Homo clades, or is primitive for the great ape and human clades (see Chapter 4). This creates a problem for the assessment of much of the later Miocene hominoid sample because morphologically similar teeth may belong to different clades. In the absence of any

information concerning the shape of the enamel-dentine junction in K.africanus this species has not been assigned to Sivapithecus. The name Kenyapithecus is already available as a generic category and will be used until the affinities of the Kenyan material can be more precisely defined.

On morphological and metric grounds there can be little doubt that M-16649 and KNM FT-46 belong in a single species. Four M^1s are assigned to this species (FT-46, -47; MB-107; M-16649) and have a range/mean (%) of 0.07, which is much less than for any living hominoid (see Table 2.5). Two M_1s were referred to this species (FT-7; MJ-5) and these have a range/mean (%) of 0.21, which is just within the range of living hominoids (see Table 2.5). The M_1 in MJ-5 is heavily worn and this may account for its small size compared to the Fort Ternan specimen, but more complete material might support the recognition of a species smaller than K.africanus (including wickeri) for the Kaloma mandible. For the present, the metrical evidence permits the assignment of the material to a single species. The upper canine (FT-39) and the lower canine (FT-28) can just be contained in this species (max/min 1.72 and 1.54 respectively, see Table 2.7). These values are at or near the maximum found in extant hominoids so that these specimens have been only provisionally referred to this species. Two central incisors (FT-49; MB-104) and a distal humerus (FT-2751) are also provisionally referred on the basis of size. The implication of this redefinition of K.africanus is that there remains no evidence for the presence of P.nyanzae at either Maboko Island or at Fort Ternan and that material in the size range of

that species, such as the Maboko postcranials, may well belong to K.africanus. The presence of a species similar in size and morphology to P.africanus at Fort Ternan (Andrews and Walker, 1976) is not disputed.

4. Gigantopithecus

(a) Gigantopithecus giganteus (Pilgrim, 1915)

Holotype: GSI D-175, right M_3 ($?M_2$)

Referred material: CYP-359/68

Synonyms:

Indopithecus giganteus (von Koenigswald, 1949)

Gigantopithecus bilaspurensis (Simons and Chopra, 1969)

This species is exemplified by the mandible described by Simons and Chopra (1969). Were it not for this specimen the holotype would be best seen as a large species of Sivapithecus. The mandible exhibits many resemblances to S.sivalensis but also shows some derived characters which are also exhibited in the Pleistocene species, G.blacki. In addition to its overall size and massive mandibular corpora G.giganteus has canines which have been functionally incorporated into the cheek tooth battery, and very small incisors. Gigantopithecus has been suggested to represent an early offshoot of the hominid clade, but the specialization of C_1 as a chewing tooth in that genus, while C_1 has become incisiform in humans, does not support this interpretation. Gigantopithecus is perhaps best seen as a specialised group with uncertain affinities but showing strong similarities to Sivapithecus, which might indicate a close phylogenetic link or may be retained primitive characters. A few fragments of teeth collected by Pilbeam's group in Pakistan may also belong to this species, although their attribution on metrical grounds is not presently possible.

5. Dryopithecus

The sample of later Miocene hominoids definitely assigned to Dryopithecus in this work comes mainly from Western Europe with large samples from Spain, Hungary and France. The sample is morphologically homogeneous, with the exception of Rud-14, and is clearly distinguished from Sivapithecus in having deep but gracile mandibular corpora, and in having dentine separation wear on the molar teeth, which wear such that dentine spots appear on each cusp separately before they fuse (previously misleading known as "thin-enamelled" wear, see Chapter 4). In a number of teeth the largest and the smallest known specimens are not sufficiently different from one another to be regarded as more than one species on the basis of comparative data (see Table 2.7). However, C^1, M^3 and all lower teeth except incisors and M_1 are more variable than is the case in living hominoids. The existance of two morphs of upper incisors further confirms that at least two species of Dryopithecus are present in addition to the unique morphology represented by Rud-14 and by IPS-41. The two species show considerable overlap in size, however, so that the assignment of specimens to species is often uncertain. There is no evidence of more than one species of Dryopithecus at Rudabanya, but two species of Dryopithecus are represented in the Spanish Miocene. Specimens have been allocated to a species primarily on the basis of size. Where size would allow the specimens to be assigned to either species the assignment is provisionally made to the most likely species. The affinities of Rud-14, which is unique in the Rudabanya sample, cannot be determined at present as it has not been

described fully. This specimen shows some intriguing resemblances to mandibles of S.meteai.

(a) Dryopithecus fontani (Lartet, 1856)

Holotype: MNHNP-AC36, mandible with C_1 - M_2

Referred material: (bracketed numbers are provisionally referred):

Associated specimens: MNHNP-1902; BMdHN 44; Rud-1, -2, -7, -12, Rud-15, -17, -44, -45; Seo de Urgel; Klagenfurt; (IPS-19), (IPS-***)

Isolated teeth:

C_1: BMdHN-45

P_3: (IPS-1a, -23)

P_4: IPS-21

M_1: IPS-38, (Rud-3), (Melchingen); (Ebingen)

M_2: BMdHN-46; Rud-11; (Salmendingen)

M_3: BMdHN-47; Rud-16, -19; (2 Trochtelfingen); (Melchingen); (brancoi type); (IPS-11)

I^1: Rud-47; IPS-12

C^1: (Rud-8)

P^3: IPS-W; (Rud-5, -10)

M^1: (Rud-6; IPS-4, -29)

M^2: (Rud-58; 2 Melchingen)

M^3: Rud-4, -13; IPS-3, -28; Lyon F-38

Synonyms:

Rudapithecus hungaricus (Kretzoi, 1969)

Bodvapithecus altipalatus (Kretzoi, 1975)

Dryopithecus fontani carinthiacus (Mottl, 1957)

Dryopithecus piveteaui (Crusafont and Hurzeler, 1961)

Sivapithecus occidentalis (Villalta and Crusafont, 1944)

Anthropodus brancoi (Schlosser, 1901)

Some specimens can be definately sexed; Rud-12 (C^1/M^1 = 0.95, see Table 2.9) is a female, Rud-15 (C^1/M^1 = 1.10, see Table 2.9) is a female), Rud-44 is proably a male, but lacks M^1, MNHNP-1902 is a male (C_1/M_1 = 1.26, see Table 2.9). Rud-14 and Rud-17 are both females (C_1/M_1 = 0.78 and 0.90 respectively, see Table 2.9). The German teeth which have variously been assigned to D.fontani and to Sivapithecus have not been examined in the original, but on the basis of casts and metrics there seems no good reason to separate them from D.fontani. The holotype of brancoi cannot be shown to be metrically distinguishable from either of the European species of Dryopithecus, but is probably a small D.fontani. The I^1 of D.fontani is low crowned with a cingulum extending a long way towards the incisive edge, but with no lingual tubercle. In this it is distinct from the I^1 of D.laietanus.

(b) Dryopithecus laietanus (Villalta and Crusafont, 1944)

Holotype: IPS-2a, partial mandible with P_3 - M_2

Referred material (bracketed specimens are provisionanlly referred):

Associated specimens: IPS-6, -8, -2, -125, (IPS-7)

Isolated teeth:

I_2: Can Llobateres

C_1: IPS-19, -18, -49

P_4: IPS-30

I^1: IPS-24, -34, -35, -36

I^2: IPS-V

C^1: IPS-39, -Y, (-16, -17, -20, -44, -50, -76)

P^3: (IPS-32, -33, -52)

P^4: (IPS-45)

M^1: IPS-37, -42

M^2: IPS-13, (-31)

M^3: IPS-10, -14, (-53)

Synonyms:

Hispanopithecus laietanus (Villalta and Crusafont, 1944)

Rahonapithecus sabadellensis (Crusafont and Hurzeler, 1961)

No specimens can be absolutely determined with regard to sex, but IPS-2 is almost certainly male (C^1/M^1 = 1.33, see Table 2.9) as is IPS-7 for which no M_1 is preserved. The upper incisors of D.laietanus differ from those of D.fontani in being high crowned with

a well developed lingual tubercle. In terms of canine size IPS-2 lies between Rud-12 and Rud-44 (female and male respectively) but in P^4 and upper molar size it is smaller than Rud-12. I have interpreted this to mean that it is a male of D.laietanus and that canines will overlap considerably between the two species. IPS-2 is at the upper end of the range for D.laietanus in all dental measurements, and overlaps to some extent with the lower end of D.fontani. This inevitably means that the attribution to species on metrical grounds is rather unreliable. Similarly IPS-7 which appears to be a male specimen has relatively small premolars for D.fontani, but has a very large canine, this specimen could be assigned to either species, but seems more likely to represent a male of D.laietanus.

6. Hominoidea incertae sedis

(a) "Sivapithecus" simonsi (Kay, 1982b)

Holotype: GSI D-298, mandible with P_3 -M_2
Referred material: M-15423; PUA- (cast M-36614).

This species was recognised to be distinct from the rest of the Siwalik forms by Simons and Pilbeam (1965). Recently specimen D-298 has been used as the holotype for Sivapithecus simonsi (Kay, 1982b) as it is the only specimen which diagnoses the species adequately, although the original has been lost for some time. Photographs and casts of the original show that M_1 had the enamel perforated through to the dentine on each cusp separately, called here dentine separation wear but previously misleadingly known as "thin-enamelled" wear. This pattern of dental wear is not seen in any other species of

Sivapithecus and is usually found in species with thin or intermediate/thick enamel (see Chapter 4) but not in species with thick enamel. Morphologically the molars of D-298 are most similar to those of the smaller specimens from Rudabanya and the larger specimens from Spain. The mandibular corpus of D-298 is deep and gracile, a situation which contradicts Kay's (1982b) definition of the genus Sivapithecus. The poorly preserved specimen M-15423 shows similar morphology and closely resembles species of Dryopithecus from Western Europe. Kay (1982b) provisionally assigned a maxilla GSI D-185 to the hypodigm of S.simonsi on the basis of its relatively small premolars and the fact that it occludes very well with a cast of D-298, as does YPM-13799. In fact the premolars of D-185 are similar in size to those of YPM-13799 and the molars are also similar in size. No metrical distinction can be drawn betwen D-185 and YPM-13799, and morphologically they are compatible. I have therefore returned D-185 to the hypodigm of S.punjabicus.

"Sivapithecus" simonsi can thus be shown to be more similar to Dryopithecus than to Sivapithecus. It is distinguished from the European species by having a very bilaterally compressed P_3, probably a primitive feature for the Hominoidea. This feature is also seen in a larger specimen housed in the Punjab University Collection (cast M-36614) which is being described by Chopra. This specimen appears to be a size variant of simonsi, and is provisionally referred to that hypodigm. There is, however, no real basis for referring simonsi to Dryopithecus. The features in common are probably retained primitive characters and where simonsi differs from

the European species, e.g. in P_3 morphology, it retains the primitive hominoid condition (see Chapter 6 for further discussion). Assigning simonsi to Dryopithecus would have the effect of making Dryopithecus a primitive "dustbin" taxon. The species simonsi may therefore warrant a separate genus when further material is recovered, but this is not justified at present. Interestingly the type of Hylopithecus hysudricus (GSI D-200) is morphologically and metrically identical to the M_1 in D-298. Other workers have regarded this specimen as a deciduous tooth, but it is unlike deciduous teeth from Pasalar or from the Siwaliks. If it is a deciduous tooth then it exhibits the way in which thickened enamel, (the main difference between deciduous and permanent teeth, resulting from the short period of development of deciduous teeth) can turn a Dryopithecus like tooth into a Sivapithecus tooth. I think that D-200 is more likely to be a permanent M_1 of a species similar to simonsi.
Hylopithecus hysudricus is retained for the type specimen only, but should generic status become warranted for simonsi, then the possibility of synonymising these two species should be considered.

(b) ? Dryopithecus

Andrews et al. (1978) described a maxilla and some isolated teeth from the Miocene of Saudi Arabia. This materia is morphologically very similar to specimens of Dryopithecus from Spain and Hungary. A description of a new species of Dryopithecus is in preparation (Andrews and Martin, in prep).

One upper canine from Spain (IPS-41) cannot be assigned to any known species of Dryopithecus. It was provisionally assigned to S.indicus (here S.sivalensis) by Crusafont and Golpe-Posse (1973). This position is not considered justified as the morphology is hardly diagnostic. The closest morphological match is in fact with the canine of the Moroto palate. The canine has not been assigned to any taxon in this work, but is evidence of a very large species, perhaps of Dryopithecus, from the Miocene of Spain.

In the course of the present work the closest morphological correlate of the Saudi Arabian material was initially considered to be the Moroto palate. The Moroto palate cannot be considered to be Proconsul major (Martin, 1981) and the possibility that it belongs to a genus with affinities with the European Dryopithecus should be considered if the original material becomes available for study.

III. SUMMARY

Sivapithecus has been shown to be widespread in deposits from the middle and upper Miocene of Eurasia. Three species have been definitely assigned to this genus; S.sivalensis and S.punjabicus from Indo-Pakistan, and S.meteai from Greece and Turkey. Two species have been provisionally assigned to Sivapithecus on the basis of their possession of molar teeth with relatively flat dentine horns, and these are S.darwini from the Vienna Basin and from Pasalar, Turkey, and S.alpani from Candir and Pasalar. On the basis of published descriptions it seems probable that two species of Sivapithecus are present in the Miocene of China, these would probably be called S.keiyuanensis and S.yunnanensis. All of the species of Sivapithecus have thick molar enamel which wears with the dentine fusion pattern of dentine exposure, and the enamel-dentine junction is relatively flat (see Chapter 4). The molars increase in size from M1 to M3, with the exception of M^3 which is smaller than M^2 in all species. S.sivalensis and S.meteai have upper central incisors which are very much larger than I^2 (I^1M-D/I^2M-D 1.80 - 2.26) and which are large relative to molar size (I^1M-D/M^1M-D 0.87 - 1.04). Upper premolars are long relative to molar length (P^3M-D/M^1M-D 0.68 - 0.76), P_3 is relatively broad compared to its length, and P_4 is long compared to M_1 length (65 - 88%). In S.sivalensis and S.punjabicus the mandible is robust (thickness/depth at M_1 0.48 - 0.60), in S.alpani the corpus is more robust (0.65) but in S.meteai the mandible is much deeper, though the same thickness as S.sivalensis resulting in a robusticity index of 0.38 - 0.49. S.sivalensis,

S.punjabicus and S.meteai have a specialised and characteristic facial morphology described in detail elsewhere (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Pilbeam and Smith, 1981; Pilbeam, 1982; Preuss, 1982; Lipson and Pilbeam, 1982; Ward and Pilbeam, 1983; Ward, Kimbel and Pilbeam, 1983).

A monospecific genus, Kenyapithecus africanus has been recognised from the later Miocene of Kenya. This species shows resemblances to Sivapithecus only in areas which reflect primitive retentions (see Chapter 6). As it cannot be shown to have any shared derived characters with Sivapithecus it was excluded from that genus until new material permits a more complete assessment of its affinities. K.africanus has molar teeth which wear with the dentine fusion pattern and which probably have thick molar enamel. Molar proportions and the size of premolars are as described for Sivapithecus. No associated incisors are known nor any details of lower facial morphology. The mandibular corpus is very robust (thickness/depth at M_1 0.64 - 0.68).

Two species of Dryopithecus are recognised from the Miocene of western Europe. D.fontani is known from France, Spain, Austria and Hungary, and D.laietanus is known only from Spain. An additional species of large hominoid is present in the Miocene of Spain but is currently known only from a single canine and its affinities cannot be assessed. Material from Saudi Arabia is referred to Dryopithecus and will be described as a new species.

A recently described species, "Sivapithecus" simonsi, does not belong to that genus. It is most similar to Dryopithecus although it was suggested that separate generic status may be warranted.

Dryopithecus molars wear with dentine separation which means that they do not have thick enamel. They may have thin enamel, intermediate/thin enamel or intermediate/thick enamel, but this can only be determined from sectioned teeth. The mandibular corpus is relatively gracile in all species (thickness/depth at M_1 0.38 - 0.55). Maxillary premolars are lengthened relative to molars as was the case for Sivapithecus, and P_4 is molarised and lengthened to an equal, or slightly greater degree than in Sivapithecus. P_3 is slightly narrower relative to length than is typical for Sivapithecus, but the ranges overlap. The exception to this is seen in the material referred to "Sivapithecus" simonsi which has a very bilaterally compressed P_3. The upper central incisor in Dryopithecus is larger than I^2 but not to nearly the same degree as in Sivapithecus (I^1M-D/I^2M-D 1.25 - 1.70) and I^1 is slightly smaller in comparison to M^1 than was the case for Sivapithecus (I^1M-D/M^1M-D 0.77 - 0.92). Dryopithecus has a facial morphology which is distinct from Sivapithecus, having a stepped nasal floor, and widely separated orbits. This morphology is seen as intermediate between Proconsul and Australopithecus showing none of the Asian specializations (Ward, Kimbel and Pilbeam, 1983; Ward and Pilbeam, 1983).

The relationships of these taxa to one another and to living hominoids are considered more fully in the final chapter of this thesis.

CHAPTER 4

ENAMEL THICKNESS IN EXTANT AND EXTINCT HOMINOIDEA

I. INTRODUCTION

A number of the problems in the interpretation of the later Miocene hominoids stem from a lack of knowledge concerning the enamel cap thickness, and the shape of the enamel-dentine junction, in extant hominoids, and of the polarity of enamel thickness changes in hominoid evolution. These data are not available, except for small samples, because obtaining them requires the destruction of some of the specimen because enamel thickness cannot be measured using X-rays since the enamel-dentine junction cannot be accurately resolved (Simons and Pilbeam, 1972; Gantt, 1977). The non-destructive method, using enamel thickness measurements from wear facets (Kay, 1981), is an indirect one which has not, until the present work, been adequately tested for accuracy.

There is a group of later Miocene hominoids which is said to be characterised by having thickened molar enamel. The existence of this group has only recently been recognised (Andrews, 1976, 1977; Pilbeam et al, 1977) and there is little consensus as to the nature of this group: whether it is a product of parallel evolution (Simons, 1976) or if it is united by a close phylogenetic relationship (Pilbeam et al, 1977; Pickford, 1977). Members of the group of "thick-enamelled hominoids" have been the most frequently proposed earliest hominids. Many characters have been used to advocate this position but most of these can be reduced to a suite of features which appear to be closely interrelated to the principal component in such discussion; thickened molar enamel, as determined by observations of

dentine exposure patterns. Implicit, and sometimes explicit in these arguments is the assumption that thick enamel is a derived character in the hominid clade. Some directly measured enamel thickness data were published by Gantt (1977) but enamel thickness has not yet been defined in metrical terms in relation to fossil hominoids and this has led to confusion regarding which species are "thick-enamelled". The morphocline polarity of enamel thickness has not been adequately determined and consequently its evolutionary significance is unclear.

This chapter is directed at the usefulness of enamel thickness for determining the relationships of the later Miocene hominoids. This will be attempted by considering what is meant by the terms "thick-enamelled hominoids" and "thin-enamelled hominoids" and by the quantification of enamel thickness in the great ape and human clade. Serial sections of human molars will be prepared so as to determine the influence of the plane of section on enamel thickness measurement. This will permit the development of a method which minimises both tissue destruction and the influence of obliquity on the enamel thickness measurements. Much larger samples of teeth of extant great apes and archaeological Homo sapiens than have previously been available will be sectioned for enamel thickness measurement. Teeth from four species of later Miocene hominoids will also be sectioned for enamel thickness measurement. Different measurements of enamel thickness will be assessed for their ability to summarise the distribution of the enamel over the tooth crown in order to select the best single figure by which to express enamel thickness. The reliability of non-destructive methods for the measurement of enamel

thickness (Simons, 1976; Kay, 1981) will be assessed for their accuracy against directly measured data. Tooth size measurements which exclude any contribution from the enamel will be used to examine the possible influence of tooth size (body size) on within species variations in enamel thickness. Kay (1981) and Gantt (1977) have shown that larger anthropoid species tend to have thicker enamel than do smaller anthropoids, and dental estimators of body size will therefore be used for scaling enamel thickness for between species comparisons. Finally the morphocline polarity and the evolutionary significance of enamel thickness changes in hominoid evolution will be discussed.

1. The concept of "thick-enamelled hominoids" and the taxonomic use of enamel thickness

Enamel thickness was first used as a taxonomic criterion by Pilgrim (1915, 1927) who observed that naturally fractured teeth of "Palaeopithecus" (here Sivapithecus) showed a considerable thickness of enamel which he considered to be a diagnostic character for the genus. The lack of comparative data and of a method for accurately determining enamel thickness in other species prevented him from using the character in the determination of phylogenetic relationships.

The first person to suggest a method whereby the thickness of enamel could be recognised by examination of tooth morphology was Butler (1956). He suggested that the functional role of thickened enamel was to modify the morphology of the occlusal surface of a

tooth. Butler (1956) believed that minor differences in the features of the tooth surface did not involve the dentine but were the result of local changes in the thickness of the enamel. He suggested that when the tooth cusps and the occlusal ridges are sharp, as is the case in the more primitive mammalian dentitions, then it is likely that the enamel is thin and evenly distributed so that the crown's external morphology reflects fairly accurately the shape of the underlying dentine surface. Where cusps are rounded, as in the human dentition, and irregular cuspules appear, he believed that the enamel would be thicker. This provided a set of criteria for recognising two categories of teeth; "thick-enamelled" and "thin-enamelled". Unfortunately Butler did not produce a survey of this character for the primates although he later published measurements of enamel thickness in broken maxillary molars of Oreopithecus (Butler and Mills, 1959).

Like Pilgrim (1915, 1927) and Butler and Mills (1959), Robinson (1956) measured enamel thickness on broken molars. He reported that the maximum visible thickness of enamel in six molars of Paranthropus robustus ranged from 1.0 - 3.0 mm with a mean of 2.3 mm. Jolly (1970a) considered teeth with thick molar enamel to be part of the "Theropithecus-complex" (T-complex). He reported that Theropithecus and Australopithecus had thick molar enamel and suggested that thick enamel was part of a suite of characters which defined hominids within the Hominoidea. Later Jolly (1970b) observed that Hadropithecus also has thick enamel on its molar teeth. This would indicate that the use of enamel thickness for taxonomy would be

difficult as thick enamel appears to have evolved in at least three distinct primate clades, and the problem of recognising instances of parallel evolution would be more likely. (Jolly, 1970a, b; Andrews, 1971).

Unworn Australopithecus and Ramapithecus teeth have high cusps, but the crowns wear nearly flat before the dentine is perforated. Simons and Pilbeam (1972) interpreted this to mean that the cusp relief in these genera must be made up almost entirely of enamel. They pointed out that it was difficult to confirm this idea non-destructively as it was not possible to resolve the enamel-dentine junction using X-rays. Simons and Pilbeam (1972) suggested that this pattern of wear provided a simple way to distinguish thick enamel from thin enamel.

Initially this dental wear pattern indicating thick enamel was considered to be restricted to Homo, Australopithecus and Ramapithecus (Simons, 1972). Simons (1972) and Pilbeam (1972) considered the thickness of enamel to be a taxonomically useful character. Simons (1972) believed that the thick enamel, marked interproximal wear, and the high wear gradient between anterior and posterior molars which Ramapithecus shared with Australopithecus and Homo justified the interpretation of Ramapithecus as being the first direct human ancestor. However, Greenfield (1974) made observations of enamel thickness, based on a small sample of broken or chipped teeth, which he suggested made enamel thickness a useless character for determining relationships within the hominoids. He reported that thick molar enamel caps were found not only in Ramapithecus, but also in

Sivapithecus indicus, S.sivalensis, Dryopithecus laietanus, Pongo and Pleistocene fossil orang-utans.

Simons (1976) elaborated on the criteria for recognising enamel thickness from observations of dental wear patterns. He determined that Dryopithecus from Europe and Proconsul from Africa as well as the extant apes had relatively thin enamel as they all showed apical cusp wear through the thin enamel at an early stage in the life of the tooth. Flattened molars with large facets that do not, for a long time, perforate into the dentine, were considered by Simons to be characteristic of "thick-enamelled" apes. This clearly reasoned procedure provided a consistent way to distinguish two categories; "thick" and "thin" provided that worn teeth were available. These categories are very broad and must necessarily blur some of the distinctions between different tooth types.

Simons (1976) believed that "the apical cusp wear, creating cusps that look like tiny volcanoes, is clearly the primitive condition for Pongidae and must have been characteristic of the ancestors of the apes with thick enamel" (Simons, 1976, page 518). By this time Simons (1976) had recognised that Sivapithecus showed a similar dentine perforation pattern to Ramapithecus as well as a high degree of interproximal wear. He argued that these were the result of a parallel adaptive strategy (presumably dietary) and that it was the wear gradient from anterior to posterior molars, which he took to indicate prolonged maturation, which, in conjunction with the other two features, demonstrated the hominoid status of Ramapithecus.

Simons (1976) also noted that once the enamel in a "thick-enamelled" tooth was perforated all of the occlusal enamel was quickly lost and the tooth crown became dentine surrounded by a thin band of enamel. He interpreted this to mean that the dentine surface underlying the enamel cap was nearly flat. This contrasts with Butler's (1956) suggestion that crown morphology is modified by variations in enamel thickness without any modification to the underlying dentine surface. These two hypotheses regarding the nature of the differences in crown morphology between "thick" and "thin-enamelled" teeth will be considered further in the light of evidence from tooth sections.

Simons (1976) therefore considered that Ramapithecus molars showed the following advances over those of earlier Miocene Dryopithecus:

a) the molars have low cusps or flattened tooth relief, coupled with thick enamel.

b) dentine does not come as far into the cusps as in early Miocene African and later Miocene European Dryopithecus.

c) wear on Ramapithecus molars produces large facets which do not perforate the dentine for a long time. When finally the enamel cap is worn away the tooth is rapidly converted into a dentine basin surrounded by an enamel rim.

It should be noted that these three characters are closely inter-related. The direct observation of wear patterns with large facets being developed before the dentine is perforated is the same observation on which the suppositions that enamel is thick and the dentine surface is relatively flat are based. Simon (1976) considers these features as being shared with Homo and Australopithecus and as

evidence for a long life span and prolonged maturation in Ramapithecus.

I consider that the detailed case for the hominid status of Ramapithecus made by Simons (1976) can be essentially reduced to the fact that this genus has molars which wear flat with very little perforation through to the dentine. The interpretations of this observation relating to enamel thickness and to the morphology of the enamel-dentine junction may be correct but it is important to realise how significant these characters became in assessing the relationships of Ramapithecus, in particular, without their ever having been tested against direct observation of enamel thickness or the morphology of the enamel-dentine junction. Equally no attempt has been made to assess the validity of Simons' (1976) interpretation of the length of the maturation period in Ramapithecus.

The discussion above may appear to be critical of Simons' (1972, 1976) and Pilbeam's (1972) approach but they deserve credit for developing the concept of "thick-enamelled hominoids" which has dominated the literature since that time. Secondly, they provided a simple and non-destructive method for sorting teeth into the categories "thick-enamelled" and "thin-enamelled", although the limits of resolution of this method should be noted when compared to metrical studies (Gantt, 1977; this work). Thirdly, Simons (1976) surveyed the hominoids using this method and found that all living hominoids, excepting humans, had the "thin-enamelled" wear pattern, while humans and some fossil hominoid species had the "thick-enamelled" wear

pattern. Simons (1976) was also the first person to directly address the problem of morphocline polarity of enamel thickness, and he came to the conclusion that "thick enamel" (as defined by wear) was a derived character in the hominid lineage but that it was also found in some non-hominid Miocene species, which he considered to be parallelisms resulting from a dietary strategy related to open country living.

It must be emphasised that the terms "thick-enamelled hominoid" and "thin-enamelled hominoid" as frequently used in the literature are defined as by Simons (1976). That is they reflect observations of the effect of wear on crown morphology and the pattern of dentine exposure. These terms are not based on metrical studies and the availability of metrical data for Pongo (Gantt, 1977) should have forced modifications to be made to these definitions. Part of the reason that the simple dichotomy continues to be accepted is undoubtedly that there is a lack of metrical data for the Middle Miocene hominoid species' enamel thicknesses. Until the present work the only directly measured data for fossil hominoid enamel thickness is the single tooth published by Gantt (1977). Thus the concept of "thick-enamelled hominoids" and "thin-enamelled hominoids" is a non-metric one, but unfortunately many discussions of this feature, and of its evolutionary significance, fail to make this point clear.

Andrews (1976) recognised that some essential features of tooth morphology held in common among species of Sivapithecus: molars with relatively bunodont cusps crowded together so that the occlusal fovea

are restricted, thick enamel on the molars, and relatively simple occlusal patterns; which were once regarded as separate characters may be part of the some character complex. Many of these characters had previously been used to support the case for the hominid status of Ramapithecus. Simons (1977) recognised that Sivapithecus and Gigantopithecus shared some "hominid" features, such as "thick enamel", with Ramapithecus and recognised that these indicated that the three genera are closely related. Simons (1977) pointed out that these resemblances might be similar responses to the same environmental pressures, i.e. parallelisms.

The idea that "thick enamel" is a derived character of hominids led workers to invoke "special pleading" explanations for its presence in species which did not fit their concept of early hominids. It was rarely considered that a feature, "thick enamel", which was argued to have evolved in parallel in more than one lineage during the Middle Miocene could not be taken as evidence for the hominid status of only one of the genera which exhibited it. Nor was the possibility considered that the morphocline polarity of enamel thickness had been incorrectly determined.

During a description of teeth from the Middle Miocene locality of Pasalar, in Turkey, Andrews and Tobien (1977) commented on the great similarity of the molars within the sample, despite major size variations. They also showed that the Pasalar molars are very similar to those of Sivapithecus indicus. They suggested that this similarity resulted from thick crown enamel and indicated that they believed that

thick molar enamel results in tooth crowns with low rounded cusps, constricted occlusal basins and indistinct occlusal ridges. Thus they considered that many of the hominid-like features of the teeth of "thick-enamelled" species could be directly attributed to enamel thickness itself. Andrews and Tobien (1977) also published the first metrical data for enamel thickness in the Pasalar teeth. The precision of such measurements, taken on chipped and broken teeth, is considered in the results section (III, 4, g) of this chapter. The importance of this data was that the larger teeth were shown to have absolutely thicker enamel than the smaller ones. This tended to confirm that "thick" and "thin" are by no means absolute divisions and that they may be obscuring important differences in enamel thickness between species of differing tooth (and therefore presumably body) sizes.

Andrews (1977) began the move towards recognition of a close phylogenetic relationship between Ramapithecus, Sivapithecus and Gigantopithecus by suggesting that they were all part of a Middle Miocene radiation of "thick-enamelled hominoids", of which Ramapithecus was still considered as the most likely ancestor of man. Pilbeam et al (1977) and Pickford (1977) went further and suggested that the "thick-enamelled hominoids" should be recognised as a biological group no part of which could be seen to be more closely related to man than any other. Pilbeam et al (1977) named a family, Ramapithecidae, containing two subfamilies; Sivapithecinae comprising Sivapithecus, Ankarapithecus, Ouranopithecus and Bodvapithecus; and Ramapithecinae containing Ramapithecus, Gigantopithecus and

Rudapithecus. The family shared a pool of characters suggesting incipient evolution towards human ancestry. These included thick molar enamel on a relatively flat dentine surface. The evidence for this was again the wear pattern of the teeth, and it carried with it the concomitant problems of the complexity of the parameter and the polarity of enamel thickness in hominoid evolution.

The concept of a later Miocene group comprised of "thick-enamelled hominoids" (as defined by wear patterns) which shared a derived character, thick enamel, with humans became well established and the position of Ramapithecus as uniquely human-like was, as a result, no longer justifiable. Andrews and Tekkaya (1980) suggested that since Ramapithecus and Sivapithecus shared the character complex associated with thick enamel on the cheek teeth then they should perhaps be considered as a single genus.

This review reveals that the concept of "thick-enamelled hominoids" is a relatively recent one and is defined not metrically but by the pattern of dental wear and dentine exposure. The terms Ramapithecidae (Pilbeam et al, 1977), Sivapithecinae (Pickford, 1977), Sugrivapithecinae (Simonetta, 1957), Gigantopithecinae (Gremyatskii, 1962) and "thick-enamelled hominoids" have been variously used to group together a number of taxa of Miocene hominoids. There has been little agreement as to which specimens belong to this group and even less consensus as to the number of taxa which are represented or how these taxa are related to one another. In particular it is unclear whether specimens assigned to this group show resemblances to one

another due to common descent (as implied in Pilbeam et al, 1977) or due to parallel evolution (Simons, 1976). Until these problems are understood it will be impossible to determine whether there is a natural (cladistic) group of "thick-enamelled hominoids".

2. The thickness of primate enamels.

The first data on enamel thickness in a sample of non-human primates was published in an abstract by Gantt (1976). He indicated that great apes have relatively thinner enamel than does Homo. This evidence, from direct measurement of histological thin sections, was preliminary confirmation that the dichotomy in wear patterns noted by Simons (1972; 1976) and Pilbeam (1972) had a basis in metrical differences in enamel thickness.

In his Ph.D thesis on the thickness of primate enamel Gantt (1977) attempted to develop a non-destructive technique for measuring enamel thickness in order that large sample sizes could be achieved for each species. He X-rayed teeth from Papio cynocephalus, Hylobates lar, and Macaca mulatta but was unable to locate a definate position for either the cusp tip or for the enamel-dentine junction. Gantt (1977) took measurements from the radiographs and checked the results against measurements taken directly from thin-sections of the same teeth and found that the measurements from radiographs varied by ± 50% of the true value. Simons and Pilbeam (1972) had previously noted that radiographs rarely resolve the enamel-dentine junction in fossilized teeth. Therefore, Gantt concluded that sectioning teeth was the only

method available which would provide accurate measurements of enamel thickness.

Gantt (1977) sectioned embedded anthropoid teeth in a buccal-lingual direction in a plane parallel to the tooth long axis (that is parallel to a plane running from the cusp tip towards the root apex). he attempted to produce sections passing through the tips of the dentine horns because these are the first areas to show enamel perforations. Gantt's (1977) major sample was for the genus Macaca (see Table 4.1), and his results for good samples of this genus provide a base line for work using necessarily smaller samples for other taxa. On the basis of this sample Gantt (1977) found that there were no significant differences between right and left teeth, but that there were differences, in some variables, between upper and lower teeth. For most of the variables, differences between individuals of one species were not significant. Gantt (1977) believed that differences in variables between six species of Macaca could be explained by scaling factors. Using an allometric equation (r=0.79) across a number of cercopithecoid taxa Gantt (1977) found that all cercopithecoid variations in enamel thickness could be explained by body size differences between the species. The one exception to this statement was Theropithecus which had relatively thick enamel for its body size. This correlation is rather a poor one and it must be emphasised that there is a considerable degree of variation in enamel thickness between cercopithecoid taxa. However, the fact the Theropithecus was found to have significantly thicker enamel than would be predicted between the very broad limits from this equation confirms Jolly's

(1970,a) non-metrical assessment of enamel thickness in this taxon. It demonstrates that thickened enamel has evolved independantly in more than one branch of the anthropoid clade by parallel evolution.

For small samples of the non-human hominoids (see Table 4.1) Gantt (1977) found that there were no significant differences between left and right teeth but there were differences between upper and lower teeth. For the molar teeth Gantt (1977) found that the enamel is thickest on the buccal surface of the lower molars and on the lingual surface of the upper molars. This distribution corresponds with the areas which are subject to the greatest biting forces (Kay, 1973) and which exhibit the greatest degree of attritional wear.

Gantt (1977) and Molnar and Gantt (1977) reported results which demonstrated that enamel thickness is variable within the "thin-enamelled" (as defined by wear patterns) extant apes. Gantt (1977) reported that Pongo has a significantly thicker enamel cap on its molar teeth than do the African apes. This agrees with the observations of Greenfield (1974) and contrasts with the evidence from Pongo's dental wear pattern which is the "thin-enamelled" one as defined by Simons (1976). When the data for Hylobates, Pongo, Pan and Gorilla were allometrically corrected and compared with data for Homo and Ramapithecus, Gantt (1977) found that the latter genera had significantly thicker enamel than apes of the same body size. Gantt (1977) also found that the average enamel thickness in Homo was absolutely greater than in any ape.

Molnar and Gantt (1977) observe that the greatest need is to establish a range of enamel thicknesses for samples of great apes. Gantt's (1977) sample sizes for each molar tooth and each species sampled are shown in Table 4.1. He presents data for only 96 molar teeth from 17 anthropoid species, and of these 34 teeth are from 5 hominoid species. The sample which Gantt (1977) had available to him provided data for only three of the six molar teeth and thus made it impossible for him to make good comparisons between enamel thickness in, for example, lower molars of one species. My aim was to sample a further 24 molars for each species of great apes and man, and if the results from this study justified it to sample a small number of representative teeth from the later Miocene "thick-enamelled hominoids" (see Materials, Measurements and Methods, and Results sections below).

Kay (1981) noted the difficulty of obtaining teeth for sectioning which had forced Molnar and Gantt (1977; Gantt, 1977) to use small samples for their enamel thickness measurements. He attempted to gain much larger samples from a wider range of species by measuring enamel thickness revealed when dentine perforations were visible. Specifically, he measured enamel thickness of the slope of the M_2 oblique cristid, which runs from hypoconid to protoconid, "proximal to the hypoconid" (Kay, 1981, page 143). If this measurement passes through the middle of the dentinal horn then it would be approximately equivalent to a measurement taken from a buccal to lingual section through the hypoconid and entoconid of a lower second molar at a level somewhere between my measurements (m) and (f) (see Figure 4.1),

probably nearer to measurement (m). Gantt (1977) sectioned teeth from buccal to lingual through the mesial cusps and I have also concentrated on this plane as it is difficult to produce a reliable section through the distal cusps of lower molars. This means that Kay's (1981) results cannot be directly checked against Gantt's (1977) or my data. Kay (1981) was careful to select teeth which had only small areas of dentine exposed on the hypoconid to avoid the problem of having the measurement position moving up and down the crown too much. Kay (1981) reports that his measurements of buccal enamel thickness on the hypoconid are very highly correlated with those reported by Gantt (1977) despite the differences just discussed and despite the fact that his method assumes either a constant conformation of the enamel-dentine junction, a situation which contradicts Simons' (1976) observations, or alternatively that enamel thickness varies little at different positions on the lateral tooth crown.

Kay (1981) found that the mean of his enamel thickness measurement was "highly" correlated with the mean of M_2 length for the species which he sampled ($r = 0.88$). From the equation of his regression line Kay (1981) calculated an "expected enamel thickness" for each species based on its mean M_2 length. He produced an index of relative enamel thickness which expressed the amount by which the measured enamel thickness differed from the predicted value as a positive or negative percentage of the predicated value. For the hominoids Kay (1981) found that Pongo has relatively thick enamel, Gorilla very thin enamel, Symphalangus syndactylus and Hylobates concolor thin enamel,

with Pan and four further species of Hylobates not differing greatly from the expected value. Several cercopithecoid species, including Theropithecus, had thick enamel, present also in Cebus. For the fossil hominoids, six specimens of Sivapithecus from Indo-Pakistan had relatively thick enamel and the range of variation among the specimens which he sampled did not exceed that found in single extant hominoid species (Kay, 1981).

Table 4.1: Published enamel thickness data samples (Gantt, 1977)

Genus	No. of species	M^1	M^2	M^3	M_1	M_2	M_3	Total
Gorilla	1	-	3	-	4	7	-	14
Pan	1	-	2	-	1	7	-	10
Homo	1	-	1	-	2	2	-	5
Pongo	1	-	1	-	2	-	-	3
Hylobates	1	-	1	-	-	1	-	2
"Ramapithecus"	1	-	-	-	-	1	-	1
Papio	1	-	3	-	3	3	-	9
Theropithecus	1	-	2	-	-	2	-	4
Mandrillus	1	-	1	-	-	-	-	1
Macaca	3	-	10	-	6	13	-	29
Cercopithecus	1	-	2	-	2	2	-	6
Presbytis	1	-	-	-	-	1	-	1
Colobus	1	-	3	-	1	3	-	7
Ateles	1	-	1	-	1	-	-	2
Alouatta	1	-	-	-	1	1	-	2
Extant hominoids	5	0	8	0	9	17	0	34
Extinct hominoids	1	0	0	0	0	1	0	1
Extant cercopithecoids	9	0	21	0	12	24	0	57
Extant ceboids	2	0	1	0	2	1	0	4
Total sample	17	0	30	0	23	43	0	96

Notes: Table compiled from Gantt (1977, Appendix).

II. MATERIALS, MEASUREMENTS AND METHODS

It has been shown that it is necessary to section teeth to take direct measurements of enamel thickness in homologous regions of the teeth. This necessarily involves the loss of some material as a result of the cutting action of the saw because it has been found to be impossible to control the plane of fracture accurately when breaking a tooth. This means that fractured sections may not expose homologous areas of the enamel and may produce oblique sections through the enamel exaggerating its thickness (see Methods section below). Boyde and Martin (1982) devised a technique which yields all of the microstructural information which can be obtained from a mature tooth in the course of sectioning it for enamel thickness measurements. This technique provides maximum information for minimum damage (see Chapter 5) and facilitated obtaining a sample of hominoid teeth for sectioning.

1. Materials

The sample for which I am presenting results is shown in Table 4.2 with the plane of section which was cut. I aimed to sample two male and two female examples of each of the six molars from the jaws of Pongo pygmaeus, Pan troglodytes, Gorilla gorilla and archaeological Homo sapiens, and I hoped to obtain unworn teeth in each case. The teeth came from the collections of the British Museum (Natural History). Teeth were extracted from specimens which are incomplete or badly damaged and/or which have no collection locality data. In this way the least useful zoological specimens from each species were

utilized to provide this new data. It was not possible to complete the samples with unworn teeth for every species, and some lightly worn teeth had to be included.

The results for the modern great apes and man suggested that it would be useful to obtain equivalent measurements of enamel thickness in fossil hominoids. Samples for this work were necessarily small, as shown in Table 4.3 but the results (for enamel microstructure as well as for enamel thickness) suggest that the gains in knowledge to be made more than compensate for the small amounts of individual teeth which must be destroyed to achieve them.

Table 4.2: Summary of the great ape and human sample used in enamel thickness and enamel microstructure research, listed according to the plane in which they were sectioned.

Genus	Tooth	Buccal to lingual	Mesial to distal
Gorilla	M^1	G 1, 13, 16	G 4
Gorilla	M^2	G 2, 5, 17	G 14
Gorilla	M^3	G 6, 15, 18	G 3
Gorilla	M_1	G 7, 10	G 19, 22
Gorilla	M_2	G 8, 11, 20, 23	
Gorilla	M_3	G 9, 21, 24	G 12
Pan	M^1	Pa 1, 4, 16	Pa 13
Pan	M^2	Pa 2, 5, 17	Pa 14
Pan	M^3	Pa 6	Pa 3
Pan	M_1	Pa 10, 19, 22	Pa 7
Pan	M_2	Pa 8, 11, 20, 23	
Pan	M_3	Pa 12, 21	Pa 9
Homo	M^1	Ho 1, 13, 16	Ho 4
Homo	M^2	Ho 2, 14, 17	Ho 5
Homo	M^3	Ho 3, 6, 18	Ho 15
Homo	M_1	Ho 10, 19, 22	Ho 7
Homo	M_2	Ho 8, 23	Ho 11, 20
Homo	M_3	Ho 12, 21, 24	Ho 9
Pongo	M^1	Po 1, 13, 16	Po 4
Pongo	M^2	Po 5, 14, 17	Po 2
Pongo	M^3	Po 3, 15, 18	Po 6
Pongo	M_1	Po 10, 19, 22	Po 7
Pongo	M_2	Po 8, 11, 20	Po 23
Pongo	M_3	Po 9, 21, 24	Po 12

Notes: Specimens are identified by codes; G 1 - G 24, Pa 1 - Pa 24, Ho 1 - Ho 24, and Po 1 - Po 24. These codes refer to individual teeth listed and identified in Appendix A.

Table 4.3: The sample of later Miocene hominoids used for enamel thickness and enamel microstructure research.

Museum no.	Site	Tooth	Taxon (see Chapter 3)
M 13365	Siwaliks	M^1	S.sivalensis
M 13366	Siwaliks	M^1	S.sivalensis
M 13367	Siwaliks	M_3	S.punjabicus
BP 4	Pasalar	M_3	S.darwini
BP 12	Pasalar	M_3	S.alpani
BP 13	Pasalar	M_2	S.alpani
BP 14	Pasalar	M_1	S.alpani
BP 17	Pasalar	M_2	S.alpani
BP 29	Pasalar	M^2	S.alpani
BP 37	Pasalar	M^2	S.darwini
BP 64	Pasalar	M_2	S.darwini

Notes: All of the fossil hominoid teeth were sectioned in a plane from buccal to lingual through the mesial cusps. The specimens from Pasalar were selected because they were unworn or only very slightly worn. Siwalik specimens were worn in some cases. Where measurements of enamel thickness have been reduced because the teeth are worn these are marked in the data tables and indicated in the text and in Figure captions.

2. Measurements

A number of measurements of tooth size have been used to assess enamel thickness in relation to tooth size. These include mesial-distal crown length, and the buccal-lingual breadth of the crown taken across the mesial cusps. A number of measurements of tooth size which exclude the contribution of enamel thickness were also used. These were: the mesial-distal length at the cervix; the buccal-lingual breadth across the mesial cusps at the cervix; the area of material (dentine and pulp) contained below the enamel-dentine junction (measurement (b), Figure 4.1) and a straight line connecting the cervical ends of the enamel-dentine junction; and the length of the enamel-dentine junction.

The discussion of the concept of "thick-enamelled hominoids" makes clear that the most useful quantification of enamel thickness would be a single figure which expresses an integrated or an average enamel thickness. There is, however, no location for a single linear measurement of enamel thickness which has been found to fulfill the role of summarising enamel thickness distributions for the entire crown. This single number concept is the attraction of Kay's (1981) relative enamel thickness measurement, but there appears to be no good reason to believe that the position at which Kay took his measurement is the single optimum description of enamel thickness for one species.

The ideal measurement of the quantity of enamel on a tooth would be the volume of the tissue. This could only be measured exactly in unworn teeth, using displacement, if the enamel cap could be separated

from the rest of the crown. This was the case for the sample studied by Korenhof (1960) which suggests that some kind of solvent method might enable one to remove the dentine from within the enamel. Enamel is laid down from the enamel-dentine junction, and the total area over which the enamel is formed, ie. the surface area of the enamel-dentine junction, is directly proportional to the number of ameloblasts, of any given size, which deposit the enamel cap (see Chapter 5). A comparison of the volume of the enamel cap with the surface area of the enamel-dentine junction would produce a linear dimension which would quantify average enamel thickness over the whole crown. However, the problems involved in separating the enamel cap from the dentine have not yet been solved. Even if they can be then the accurate measurement of the surface area of the enamel-dentine junction presents technical problems, given its complex topography, which are beyond the scope of this work.

In the present work the ideal ratio of enamel volume to enamel-dentine junction area is approximated from a comparison of the area of enamel, exposed in a section, with the length of the enamel-dentine junction over which the thickness is developed. This has the same effect of producing an average enamel thickness over the crown, but in this case the measurements are restricted to the plane of section which is cut. In addition I have taken a number of linear measurements which are assessed for their ability to provide a useful summary of the distribution of the enamel. If a good description can be obtained from a single linear measurement, as Kay (1981) suggests, then this would greatly faciliate the acquisition of enamel thickness

data using non-destructive methods (such as wear facets) or minimally destructive methods such as core drilling. The measurements of enamel thickness which I have used are listed in Table 4.4. The positions and orientations of the measurements are shown in Figures 4.1 and 4.2. The purpose of the measurements is explained below.

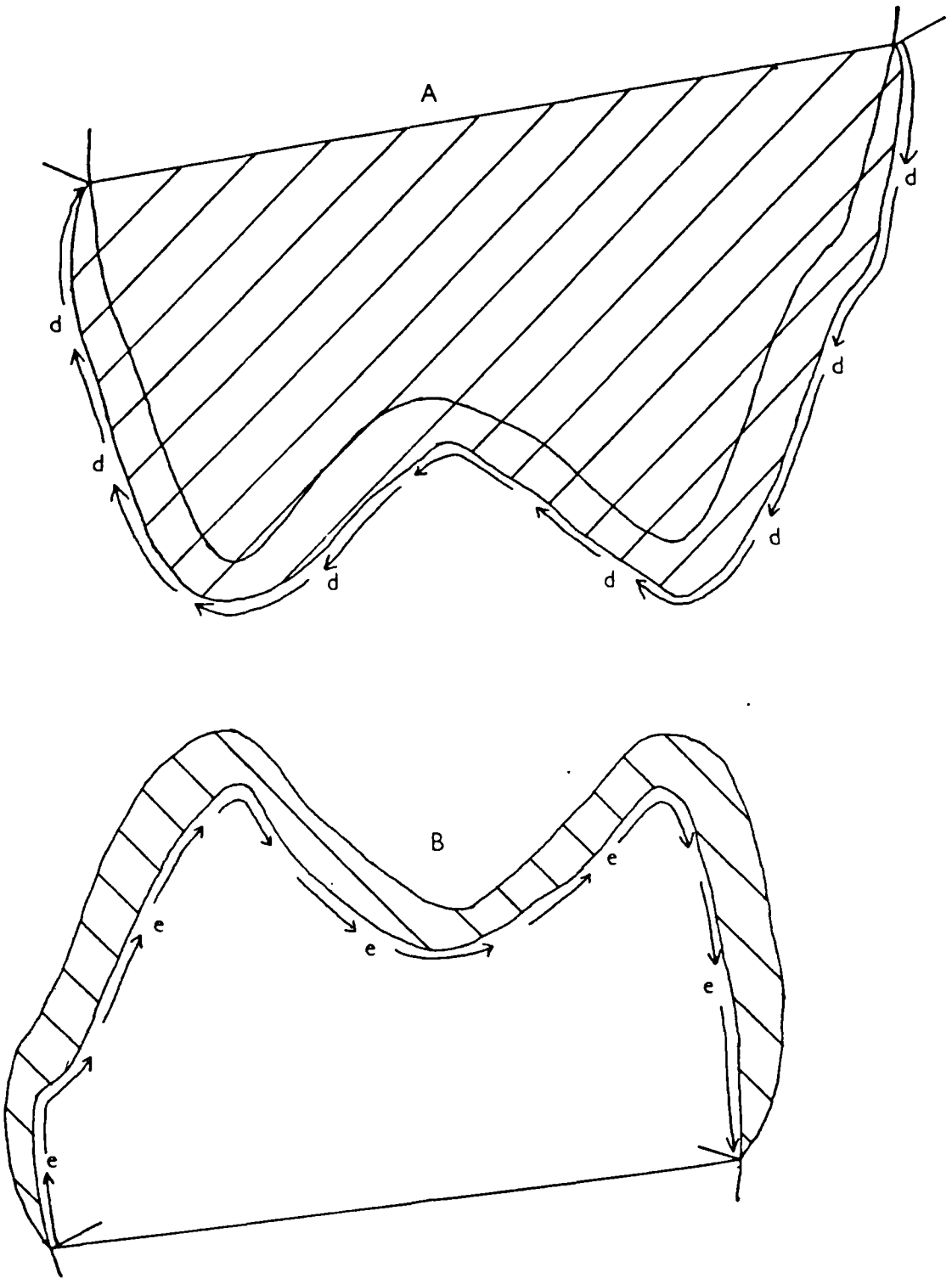
Area of section (a): This is a measurement of the total area of tissue enclosed in the tooth section (Figure 4.1.). In other words the area enclosed by the outer limit of the enamel cap buccally, occlusally and lingually and a straight line connecting the position of the cervix of the tooth buccally and lingually.

Area under the enamel-dentine junction (b): The area enclosed by the enamel-dentine junction running from the cervix on the buccal side, over the dentine horns and to the cervix on the lingual side with a straight line connecting the two cervixes (Figure 4.1). This measurement gives a measure of total tooth crown size excluding the contribution of the enamel cap.

Area of the enamel cap (c): This is the difference between the area of the section (a) and the area under the enamel-dentine junction (b) (Figure 4.1). This is used as a single measurement which summarises the distribution of enamel over the entire tooth crown in the plane of section.

Length along the outside of the enamel (d): This measurement is the perimeter length of the outside of the enamel cap (Figure 4.1)

Figure 4.1: Area and perimeter measurements of tooth sections.



The shaded area in drawing A is measurement (a) (Table 4.4). The shaded area in drawing B is enamel cap area (measurement c, Table 4.4), the unshaded area in drawing B is dentine area (measurement b, Table 4.4).

measured from the buccal cervix across the cusp tips and down to the lingual cervix.

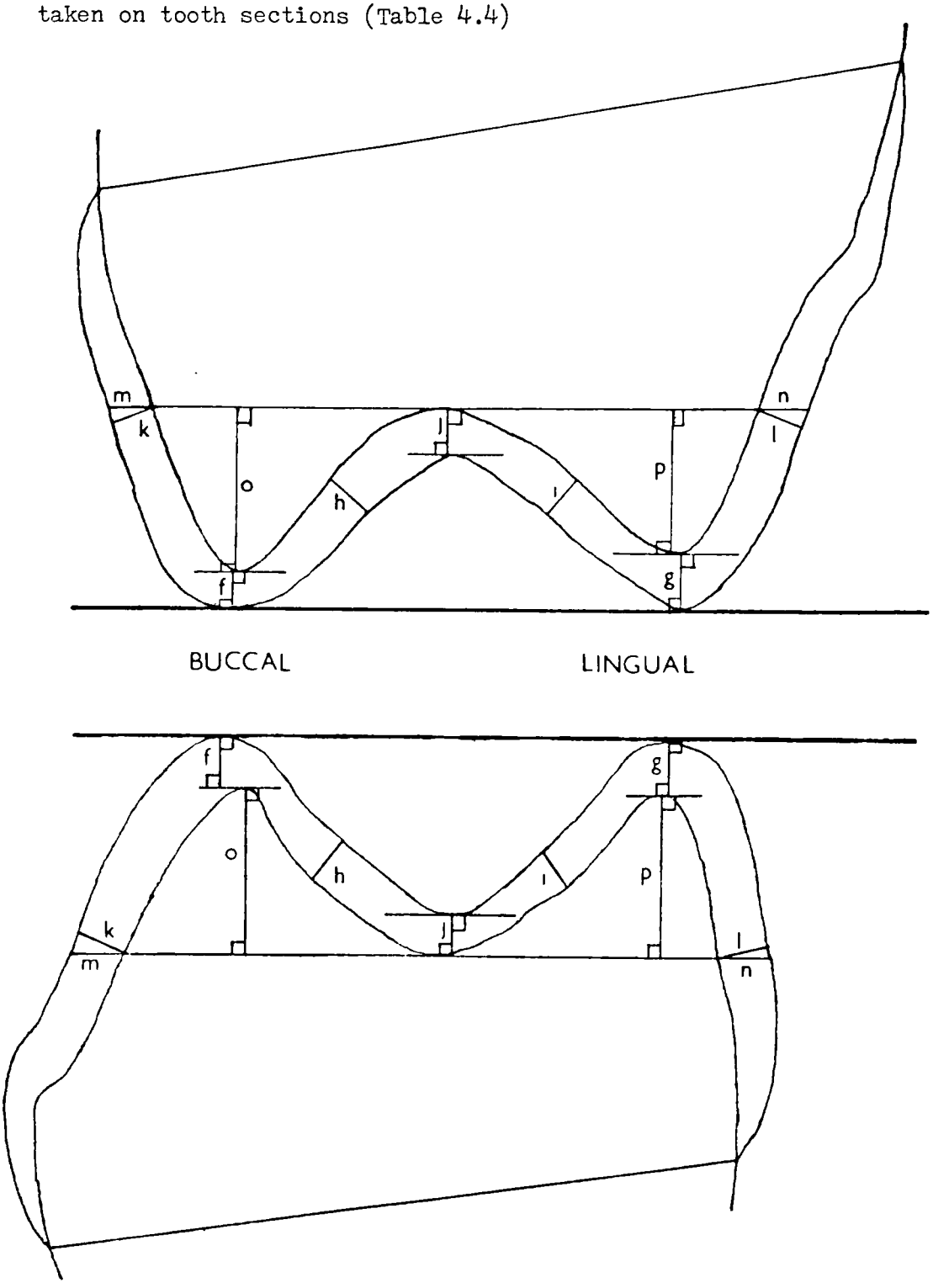
Length of the enamel-dentine junction (e): This measurement begins and ends at the same points as the length along the outside of the enamel (d) (Figure 4.1) but goes along the enamel-dentine junction rather than the outside of the enamel.

Vertical thickness of enamel on the buccal cusp tip (f): This measurement (Figure 4.2) quantifies the vertical thickness of enamel from the tip of the dentine horn to the tip of the cusp and measures how much enamel must be worn away, in a horizontal plane, before dentine is exposed on the buccal cusp tip.

Vertical thickness of enamel on the lingual cusp tip (g): This measurement (Figure 4.2) quantifies the vertical thickness of enamel from the tip of the dentine horn to the tip of the cusp and measures how much enamel must be worn away, in a horizontal plane, before dentine is exposed on the lingual cusp tip.

Radial enamel thickness on the occlusal (lingual) face of the the buccal cusp (h): This measurement is taken from the enamel-dentine junction to the enamel surface on the occlusal (lingual) face of the buccal cusp. On upper molars wear facets do not develop in a horizontal plane on the buccal cusp, they develop on the occlusal face of the buccal cusps and it this aspect of the buccal cusps which is usually first perforated through to the dentine. This measurement

Figure 4.2: The position and orientation of the linear measurements taken on tooth sections (Table 4.4)



(Figure 4.2) attempts to quantify the thickness of enamel on the occlusal (lingual) face of the buccal cusp which must be worn away before dentine is exposed on this face.

Radial enamel thickness on the occlusal (buccal) face of the lingual cusps (i): This measurement (Figure 4.2) is taken from the enamel-dentine junction to the enamel surface on the occlusal (buccal) face of the lingual cusp and attempts to quantify the thickness of enamel on the occlusal (buccal) face of the lingual cusp which must be worn away before dentine is exposed on this face. The same reasons apply as for the radial thickness of the enamel on the occlusal (lingual) face of the buccal cusp (measurement, h) but with reference to lower molars.

Vertical thickness of the enamel in the middle of the occlusal fovea (j): This measurement (Figure 4.2) is taken from the base of the occlusal enamel to the outer surface of the enamel and quantifies the vertical thickness of the enamel in the middle of the occlusal fovea. On crenulated teeth it is sometimes difficult to establish a plane which may be regarded as the top of the enamel surface because deep and wide midline folds and grooves may be present. When this is the case the measurements of occlusal enamel thickness on the cusps (h and i) provide alternative measurements of occlusal basin enamel thickness.

Radial thickness of the enamel on the mid-lateral aspect of the buccal cusp (k): This measurement (Figure 4.2) is taken from the

enamel-dentine junction to the outside of the enamel and is a radial (minimum) quantification of the thickness of the enamel on the lateral aspect of the buccal cusp at the level of the base of the occlusal enamel. It can be compared to the horizontal measurement at the same point (m) to establish how accurately estimates of enamel thickness made from molars worn to the point where little or no occlusal enamel remains reflect radial thickness.

Radial thickness of the enamel on the mid-lateral aspect of the lingual cusp (l): This measurement (Figure 4.2) is taken from the enamel-dentine junction to the outside of the enamel and quantifies the radial (minimum) thickness of the enamel on the lateral aspect of the lingual cusp at the level of the base of the occlusal enamel. It can be compared to the horizontal measurement at the same point (n) to establish how accurately estimates of enamel thickness made from molars worn to the point where little or no occlusal enamel remains reflect radial thickness.

Horizontal thickness of enamel on the mid-lateral aspect of the buccal cusp (m): This measurement (Figure 4.2) is taken from the enamel-dentine junction to the outside of the enamel and quantifies the horizontal thickness of the enamel on the lateral aspect of the buccal cusp at the level of the base of the occlusal enamel. This is an oblique measurement but one which corresponds with the section through the enamel thickness which would be exposed by attritional wear.

Horizontal thickness of enamel on the mid-lateral aspect of the lingual cusp (n): This measurement (Figure 4.2) is taken from the enamel-dentine junction to the outside of the enamel and quantifies the horizontal thickness of the enamel on the lateral aspect of the lingual cusp at the level of the base of the occlusal enamel. This is an oblique measurement but one which corresponds with the section through the enamel thickness which would be exposed by attritional wear.

Vertical height of the dentine horn of the buccal cusp (o): This is a measurement of the vertical distance between the tip of the dentine horn of the buccal cusp and the base of the occlusal fovea enamel (Figure 4.2). It is used to assess the contribution of enamel and dentine separately to the cusp height in order to test Simons' (1976) suggestion that the dentine surface is relatively flat in "thick-enamelled" species.

Vertical height of the dentine horn of the lingual cusp (p): This is a measurement of the vertical height of the dentine horn of the lingual cusp from the tip of the horn to the level of the base of the occlusal fovea enamel (Figure 4.2).

All of the measurements are in metric units: millimeters in the case of the linear dimensions ((d) - (p)) and mm^2 in the case of the area measurements ((a) - (c)).

Some of these measurements are combined to produce indices. The area

of the enamel cap (c) is divided by either length of the enamel-dentine junction (e) or the area below the enamel-dentine junction (b); these produce an average enamel thickness measurement in the first case (c/e) which approximates the ideal ratio between enamel cap volume and the surface area of the enamel-dentine junction. In the second case (c/b) the index is dimensionless and may therefore be difficult to interpret. Both measurements correct the magnitude of the area of the enamel cap for both the height and the width of the tooth crown. Thirdly the perimeter length of the enamel cap (d) is divided by the length of the enamel-dentine junction (e) to produce a dimensionless index. This is similar to comparing the circumferences of two concentric circles which gives a figure directly proportional to a ratio of their radii. In this case the relationship is more complex, but the principle may be similar. The average enamel thickness (c/e, Figure 4.1) is considered on a priori grounds to be the best description of enamel thickness in the plane of section, this supposition is evaluated below.

Table 4.4: Letters used to identify enamel thickness measurements in Figures 4.1 and 4.2, Appendix A and in the text. The measurements can be more fully understood by reference to Figures 4.1 and 4.2 and to the more complete definitions in the text.

	Definition
a)	Area under the enamel (mm^2)
b)	Area under the enamel dentine junction (dentine area) (mm^2)
c)	Area of the enamel cap (a - b)(mm^2). (Gantt, 1977; R)
d)	Length along the outside of the enamel cap (mm)
e)	Length along the enamel-dentine junction (mm)
f)	Vertical thickness of the enamel over the buccal cusp tip (mm). (Gantt, 1977; A)
g)	Vertical thickness of the enamel over the lingual cusp tip (mm). (Gantt, 1977; B)
h)	Radial (minimum) thickness of the enamel at the mid-point of the occlusal (lingual) face of the buccal cusp (mm). (Gantt, 1977; EA)
i)	Radial thickness of the enamel at the mid-point of the occlusal (buccal) face of the lingual cusp (mm). (Gantt, 1977; EB)
j)	Vertical thickness of the enamel in the centre of the occlusal fovea (ignoring deep grooves) (mm). (Gantt, 1977; E)
k)	Radial thickness of the mid-lateral enamel on the buccal cusp at the level of the base line of the occlusal enamel (mm). (Gantt, 1977; JJ)
l)	Radial thickness of the mid-lateral enamel of the lingual cusp at the level of the base line of the occlusal enamel (mm). (Gantt, 1977; KK)
m)	Horizontal thickness of the enamel on the mid-lateral buccal cusp (mm). (Gantt, 1977; J)
n)	Horizontal thickness of the enamel on the mid-lateral lingual cusp (mm). (Gantt, 1977; K)
o)	Vertical height of the dentine horn of the buccal cusp (mm). (Gantt, 1977; C)
p)	Vertical height of the dentine horn of the lingual cusp (mm). (Gantt, 1977; D)

Notes: Where my measurements correspond with ones used by Gantt (1977) the definition of the measurement is followed by (Gantt, 1977; ?), in the place of the query is the capital letter used by Gantt (1977) and Molnar and Gantt (1977) to identify enamel thickness measurements.

3. Methods

The teeth to be sectioned were mounted on a block using a dental wax which hardens on cooling. The specimen was oriented over the stationary saw blade and its position adjusted while the wax was still ductile. In this way the centre of the saw blade was directly alligned with the tips of the mesial cusps. The vertical plane of the specimen was adjusted so that the plane of section would be parallel to the long axis of the tooth (i.e. from cusp tip to root apex). A Buehler wafering saw was used to make the cut. The saw blade destroys 350 μm of material so that each cut produces two faces on which enamel thickness can be measured 350 μm apart.

Each of the cut faces exposed by the saw cut was photographed to provide a permanent record and the measurements were taken from the photographs. The photographs were taken at a standard magnification and with standardised orientation. This was achieved by mounting the sections on a glass slide with the cut face against the glass. The glass slide had a scale with half millimeter divisions marked on it permanently attached to it with the scale against the glass, thus ensuring that the scale and the cut section are coplanar. The section was then photographed using a single lens reflex camera on an automatic bellows attached to a focusing track and a macro-stand. The glass slide was mounted on the macro-stand and the section photographed through the glass slide. This system ensures that the section and the scale are exactly parallel with the film plane. The bellows were prefocused on the photographic scale at a magnification which allowed the largest specimen to fit the negative size. The

method of mounting the sections on the back of a glass slide means that there was no need to adjust the focus between shots so that each negative was recorded at a standard magnification. The photographs were printed at a constant magnification providing photographs of the tooth sections all at the same magnification which greatly facilitated measurement.

In some specimens the enamel and the dentine were very similar in colour and the enamel-dentine junction was not clearly visible. In these cases the specimens were coated with gold using a sputter coater (see Chapter 5) and then etched with 0.5% $H_3 PO_4$ for 30 seconds which removes the gold from the enamel but leaves it on the dentine. This method is a useful one for enhancing contrast where necessary (Figure 4.13e).

Measurements (a) - (e) (Figure 4.1) were recorded using a pen transducer attachment to a micro computer. Two tracings were made, the first along the outside of the enamel cap (measurement (d), Figure 4.1) and the second along the enamel-dentine junction (measurement (e), Figure 4.1). The computer calculates both the length of the line traced and the area enclosed by the lines traced after connecting the ends of the lines traced with a straight line. The trace along the outside of the enamel (Figure 4.1 (d)) produces measurements (a) and (d) (Table 4.4, Figure 4.1). The trace along the enamel-dentine junction (Figure 4.1 (e)) produces measurements (b) and (e) (Table 4.4, Figure 4.1). Measurement (c) (Table 4.4, Figure 4.1) is obtained by subtracting measurement (b) from

measurement (a). Measurements (a) - (e) (Figure 4.1) are independent of the orientation of the photograph. Measurements (f) - (p) are linear measurements whose orientation is defined relative to a selected standard plane for the tooth section. There is no naturally occuring plane which can be selected on a priori grounds. For this work the photographs of the tooth sections were alligned so that the tips of the cusps were alligned in a horizontal plane. The measurements were taken at the positions and with the orientations shown in Figure 4.2, using dial callipers, to the nearest 0.1mm. The photographs were all printed at 8.48 times life size so that the life size measurements were recorded to the nearest 0.012mm.

Errors

A number of tracings, from which the area and perimeter lengths were calculated ((a) - (e), Figure 4.1), were repeated ten times to calculate the tracing error; for a mean area of 124mm^2 the standard deviation of the meausrements is 0.77 mm^2 (95% confidence limits 122.26 - 125.74); and for a mean length of 33.18mm the standard deviation of the measurements is 0.117mm (95% confidence limits 32.92 - 33.44).

III. RESULTS

1. Introduction

In this section results are presented for serial sections of some teeth. These show that there is a potential problem in taking measurements from sections which have cut through the enamel cap obliquely. This problem is resolved by consideration of ways to recognise which of the two faces revealed by the saw cut produces the less oblique section. The measurements of enamel thickness are then presented with a consideration of ways by which enamel thickness measurements can be scaled to take account of differences in tooth size between the species sampled. Different measurements of enamel thickness (Figures 4.1 and 4.2) are assessed for consistency with the measurement of average enamel thickness ((c/e), Figure 4.1). Finally a measurement of relative enamel thickness taking account of size is defined and results presented which allow comparisons of enamel thickness between species to be made.

One of the problems encountered by Molnar and Gantt (1977; Gantt, 1977) was the precise location of the tips of the dentine horns. Gantt (1977) cut a number of sections in order to locate the tips of the dentine horns because he found that a single cut was unlikely to be correctly located. Unfortunately he does not provide data for more than one of these sections which would have enabled one to assess the effect of taking measurements on a section which does not pass exactly through the tips of the dentine horns. It is desirable to limit the number of cuts made as each cut destroys material.

2. Serial Sections

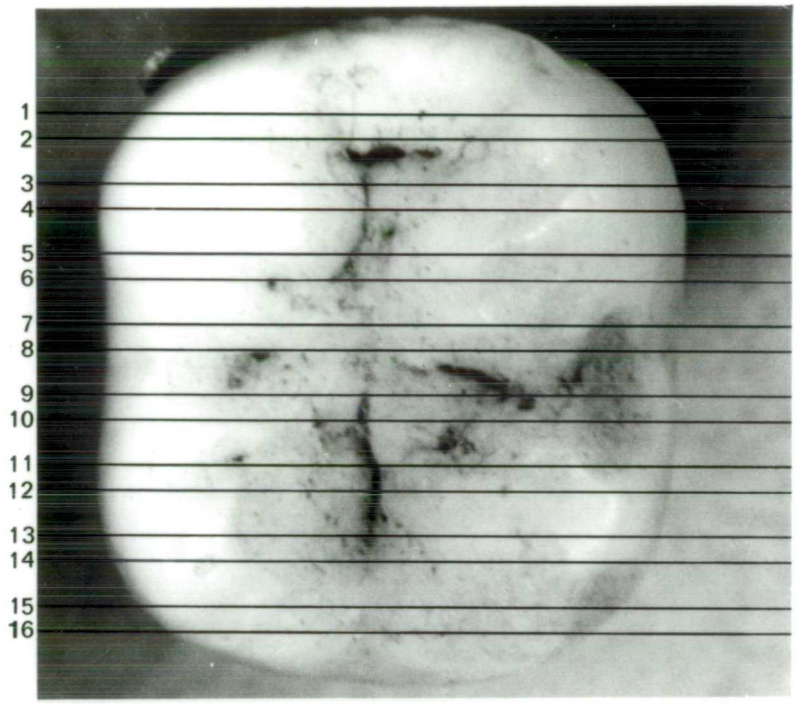
In order to assess the magnitude of errors in enamel thickness measurement which might result from imperfect sectioning one upper and one lower human molar were serial sectioned. The teeth were mounted and positioned as described in the Methods section so that the centre of the saw blade was directly alligned with the tips of the mesial cusps. This position is described as the primary cut. The teeth were then retreated in 1mm steps on the Buehler wafering saw and the first cut was made as close as possible to the mesial end of the tooth. After each cut the specimen was advanced exactly 1mm. The saw blade destroys 350 μm of material so that each cut produces two faces on which enamel thickness can be measured 350 μm apart. The wafers cut are then 650 μm thick so that enamel thickness measurements are made at 350 μm and 650 μm intervals along the entire length of the teeth being serial sectioned (see Figure 4.3).

The sections of the upper second human molar are shown in Figure 4.4, those of the lower second human molar in Figure 4.5. The variation in magnitude of the enamel thickness measurements are shown in Figures 4.6 and 4.7, where the numbers on the x-axis indicate the position of the measurement along the mesial-distal axis of the teeth as shown in Figure 4.3. Both upper and lower molars will produce enamel thickness measurements of considerably varying magnitude according to the position of the buccal-lingual cut along the mesial-distal axis of the tooth. Figures 4.6 and 4.7 are marked with a pair of vertical lines which indicate the two faces which would have

been revealed by the primary cut; i.e. the cut made by the saw blade when alligned with the tips of the cusps externally. In the case of the linear measurements (f) - (n) the enamel thickness on one or other of these two faces is at or near the minimum for the whole length of the crown.

The variation in enamel thickness measurements along the mesial-distal axis of the tooth may be the result of two factors. Firstly it may reflect real differences in thickness between occlusal basin enamel and cuspal enamel; secondly it is at least partly the result of the sections cutting through the enamel cap obliquely. Figure 4.8 shows a mesial-distal section through the buccal cusps of a lower molar. A measurement of the vertical thickness of the enamel will vary according to the position of the cut face along the mesial-distal axis of the tooth even when there are no differences in radial thickness. The radial thickness of the enamel is shown as a dotted line for sections 2 and 3 in Figure 4.8, and only section 1 is a true cross section; i.e. the vertical thickness is equal to the radial thickness in this plane. The same problem applies equally to horizontal measurements of cuspal enamel thickness (i.e. those taken at a level cuspal to the line connecting measurements (m) and (n) in Figure 4.2). This is shown in Figure 4.9 which is a generalized plan view through a cusp. Measurements of enamel thickness which are taken in a plane which does not pass through the maximum diameter of the dentine horn are exaggerated as a result of the obliquity of the section.

Figure 4.3: Human molars used for serial sections. The lines indicate the planes of faces which were used for enamel thickness measurements. The numbers of the lines correspond with those in Figures 4.4 - 4.7. The narrowly spaced lines are 350 µm apart and the portion of the tooth between them was lost by the cutting action. The widely spaced lines are 650 µm apart and the portions between them are the sections of tooth which remained. The buccal side of each tooth is indicated by a black spot.



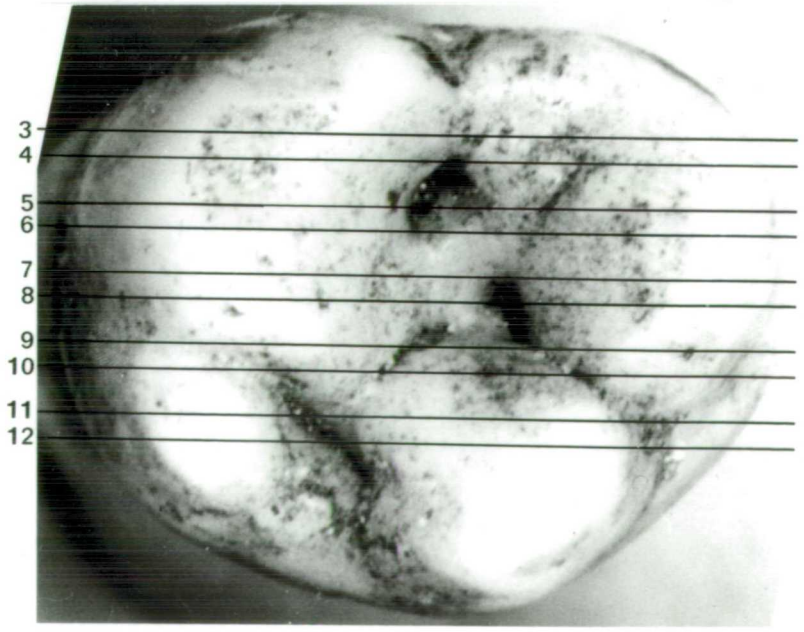


Figure 4.4: Serial sections of Homo M^2 (Ho 17). Face numbers correspond with the planes of section in Figure 4.3. A black spot indicates the buccal side of the tooth.

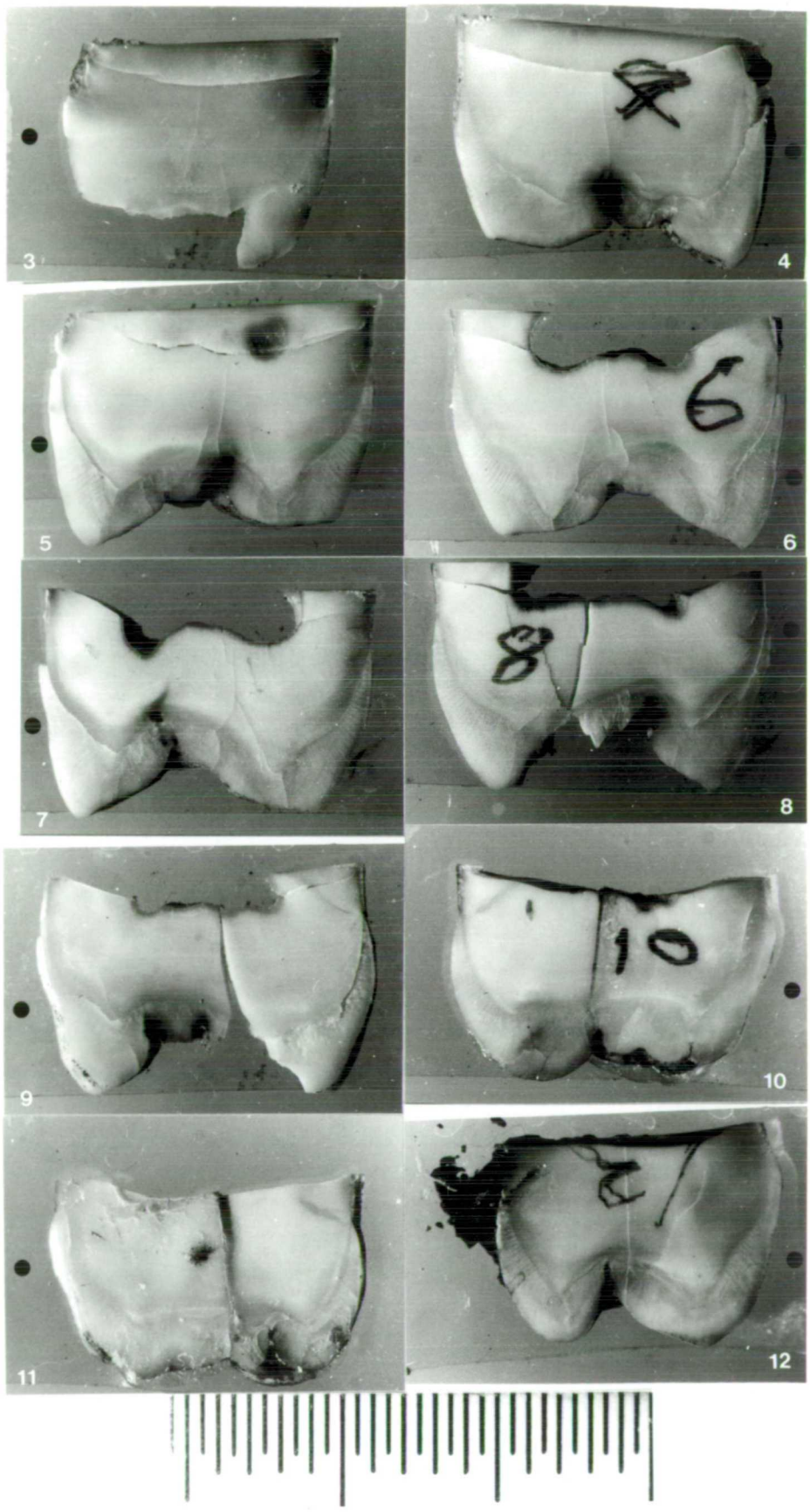
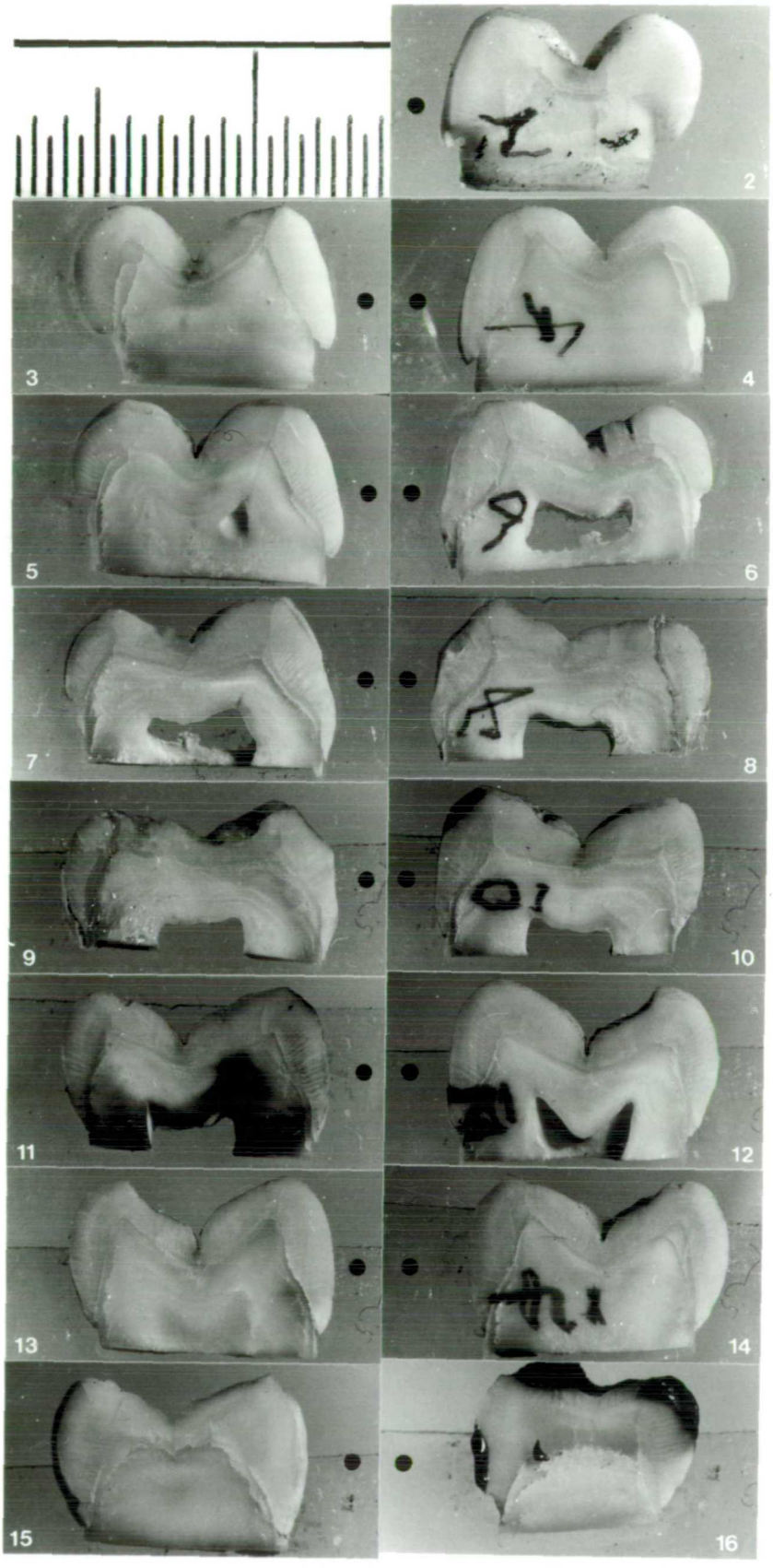


Figure 4.5: Serial sections of *Homo* M_2 (Ho 23). Face numbers correspond with the planes of section in Figure 4.3. A black spot indicates the buccal side of the tooth.



The serial sections of both upper and lower human second molars can also be used to examine the extent of variation resulting from different positioning of the sections. The measurement which shows least variation along the crown length is the index of enamel cap perimeter length ((d), Figure 4.1) divided by the length of the enamel-dentine junction ((e), Figure 4.1). However, the least variable measurement is not necessarily the best one as two influences may be present; the influence of oblique sectioning and the influence of real variation in the radial thickness of the enamel over different parts of the tooth; and these inflences may cancel each other out so as to reduce the observed variability. For example, the vertical measurements of enamel thickness ((f) and (g), Figure 4.2) would increase when the plane of measurement is not coincident with the plane of the maximum diameter of the dentine horns (Figure 4.8). If the radial thickness of enamel is less in the occlusal basin than it is over the cusp tips then these two influences would tend to cancel one another out to some extent. What is necessary, therefore, is to separate out the influence of obliquity from real differences in radial enamel thickness.

In general the index of average enamel thickness (enamel cap area (c), Figure 4.1, divided by enamel-dentine junction length (e), Figure 4.1; hereafter referred to as (c/e) or average enamel thickness, varies less than do the linear measurements of occlusal enamel thickness ((f) - (j), Figure 4.2) which suggests that this index is less prone to errors resulting from obliquity. Similarly the lateral enamel thickness measurements ((k) - (n), Figure 4.2) vary

less than do the occlusal measurements along the mesial-distal axis of the tooth. This is no doubt because the low lateral enamel is not being sectioned obliquely. The conical model (Figures 4.8 and 4.9) only applies to cuspal enamel as the lateral enamel forms a continuous band around the whole tooth. This in turn suggests that if heavily worn teeth (i.e. those with little or no occlusal enamel remaining) are utilised to estimate low lateral enamel thickness ((k) - (n), Figure 4.2, for example) then the measurement procedure would be less prone to errors resulting from small mesial-distal variations in the plane of measurement than if less worn teeth are used, such as those used by Kay (1981) which ensured that cuspal enamel was measured.

The most important inference to draw from the serial sections is that the exact position of the buccal-lingual plane of section along the mesial-distal axis of the tooth is critical if the influence of obliquely sectioned enamel thickness is to be avoided. Effectively, each cusp consists of a conical dentine horn overlain by a casing of enamel. The measurement which best describes this situation is a radial measurement of skin thickness. It is most convenient for the purposes of measurement if the radial dimension of enamel thickness is coplanar and coincident with the plane of section. As shown in Figure 4.9 section 1 produces this situation while sections 2 and 3 would be more difficult to use to obtain a measurement of radial enamel thickness. Therefore, the section which is required is one which passes through the maximum breadth of the dentine; i.e. one which follows a diameter of the dentine cone.

Figure 4.6: Variation in enamel thickness measurements (Figs. 4.1 & 4.2, Table 4.4) along the mesial to distal length of a human M^2 (Ho 17). The face numbers on the x-axis correspond to those in Figs. 4.3 & 4.4.

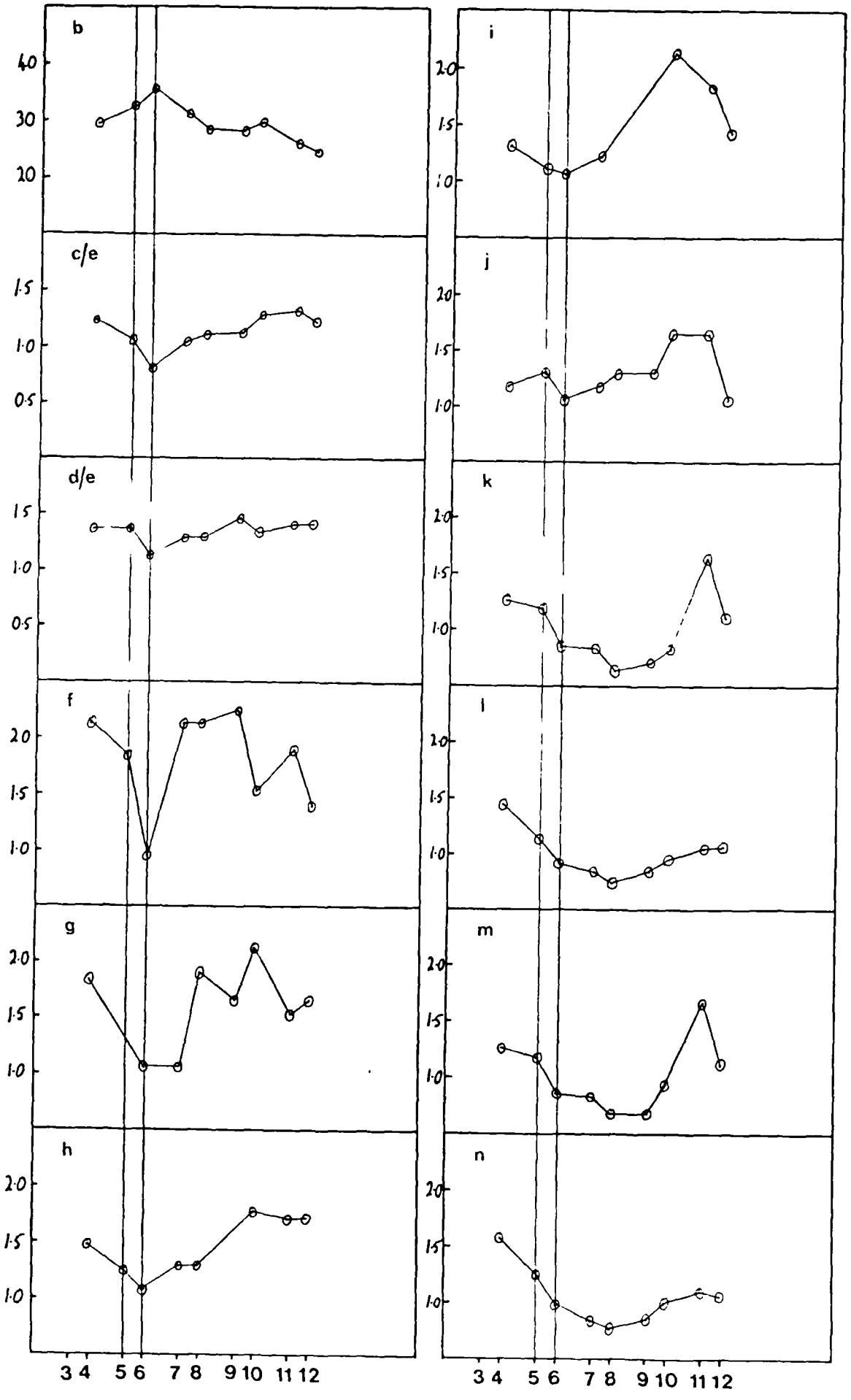


Figure 4.7: Variation in enamel thickness measurements (Figs. 4.1 & 4.2, Table 4.4) along the mesial to distal length of a human M_2 (Ho 23). The face numbers on the x-axis correspond to those in Figs 4.3 & 4.5.

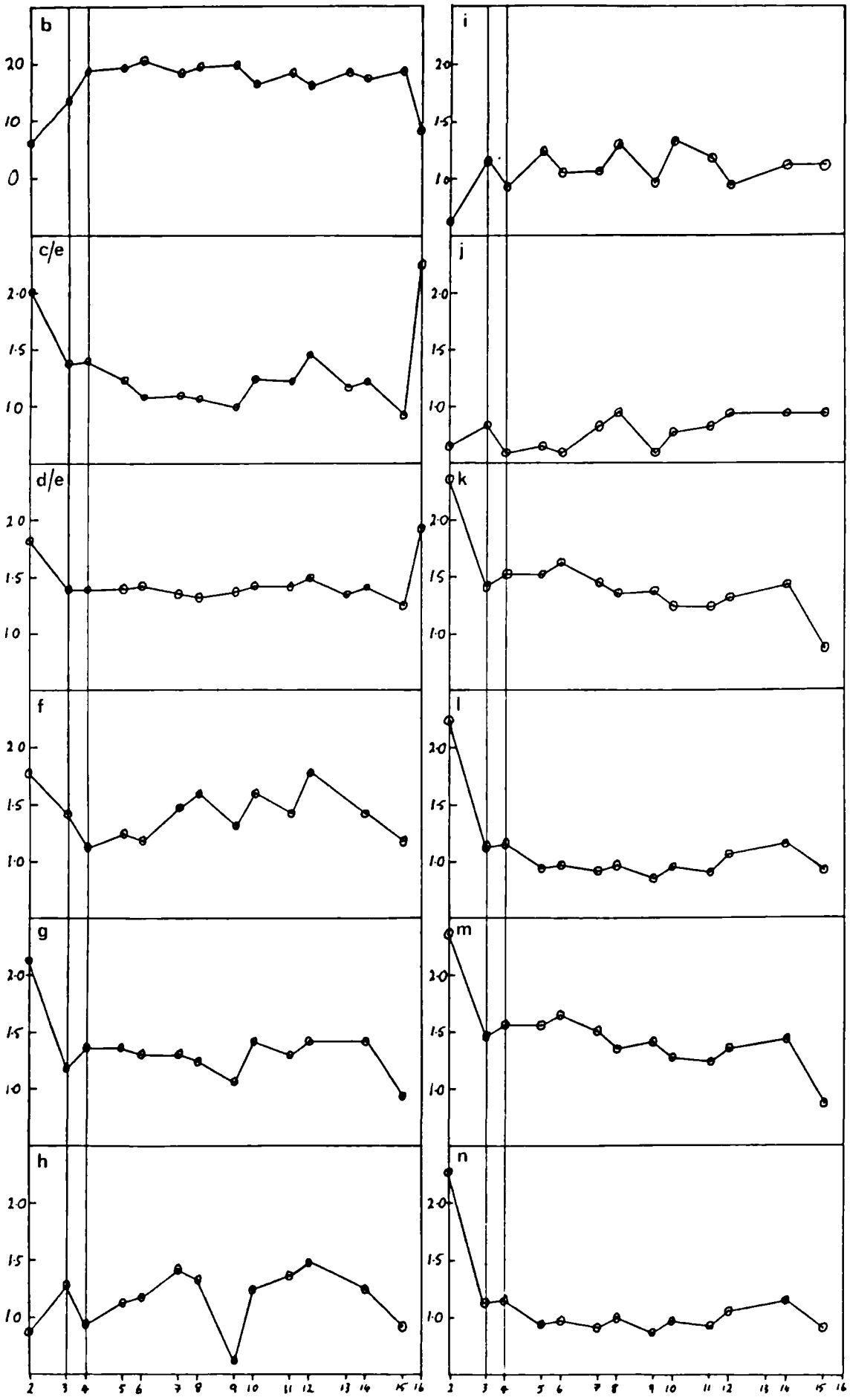


Figure 4.8: A mesial to distal section of a lower molar showing the effect of oblique sections on the apparent enamel thickness. Section 1 reveals the true radial (minimum) cuspal enamel thickness. Sections 2 and 3 produce oblique sections of the enamel thickness, the radial thicknesses are indicated by broken lines. The apparent enamel thickness revealed by the sections is shown in the three columns. The sections which do not pass through the tip of the dentine horn (2 & 3) produce exaggerated enamel thickness measurements.

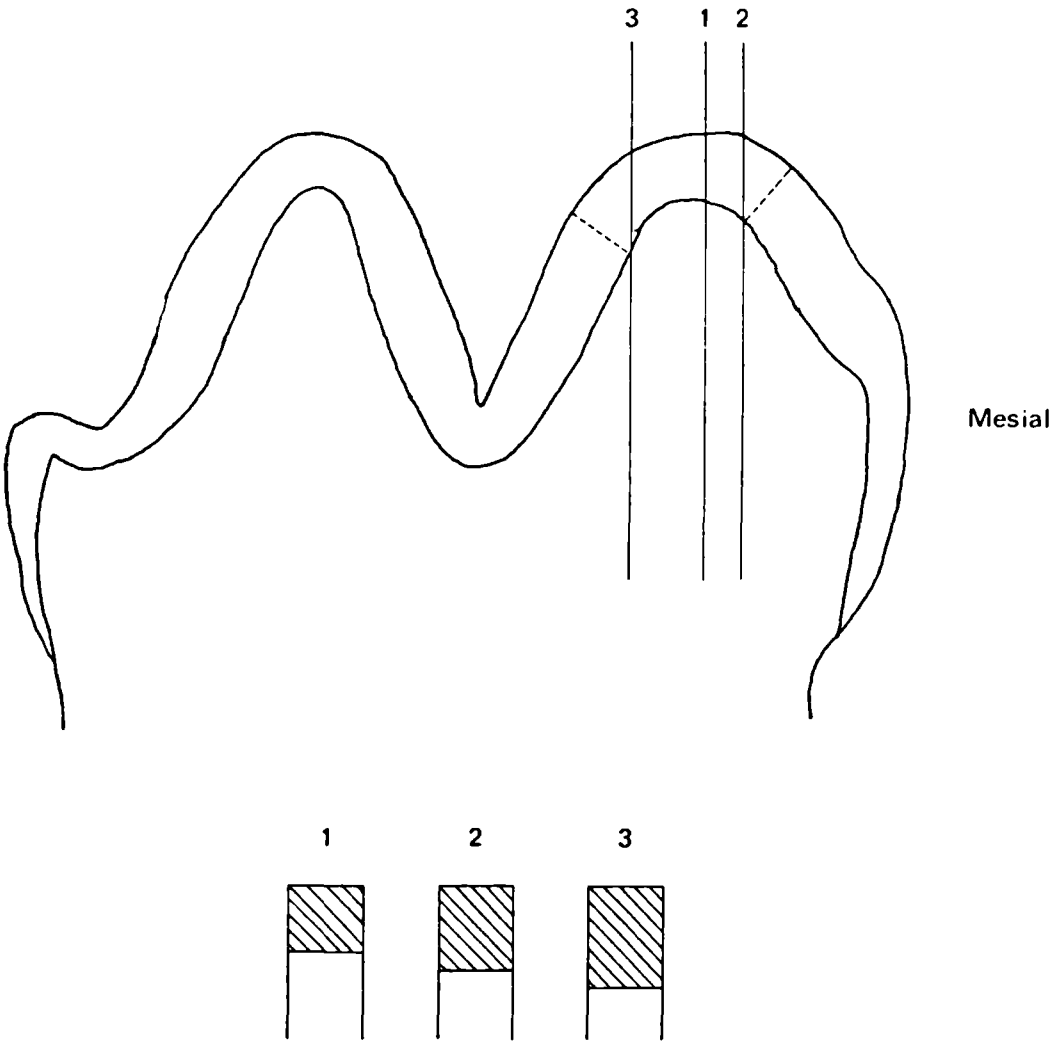
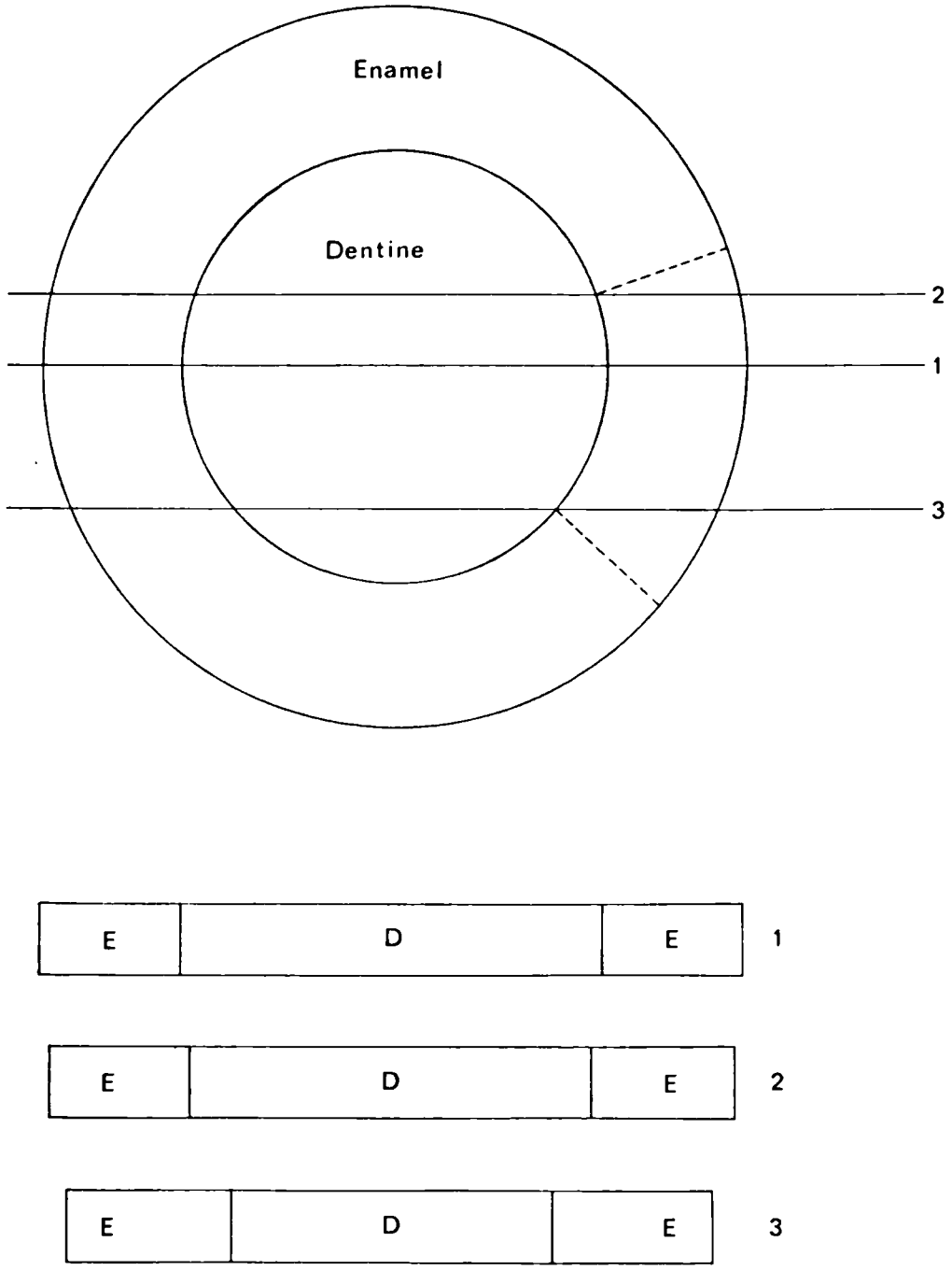


Figure 4.9: Hypothetical plan view through a cusp showing the difference in apparent enamel thickness between radial and oblique sections.



Section 1 follows a diameter and reveals the true radial thickness of the enamel, in this case the dentine dimension is a maximum. Section 2 and 3 cut the enamel obliquely, the radial thicknesses are indicated by broken lines. When the section is oblique (2 & 3) the enamel component is exaggerated and the dentine dimension is underestimated. Only a section revealing the maximum of the dentine horn produces a true radial enamel thickness. The radial thickness is the minimum value which can be observed in a section, no plane of section can underrepresent the enamel thickness.

3. Oblique Sections

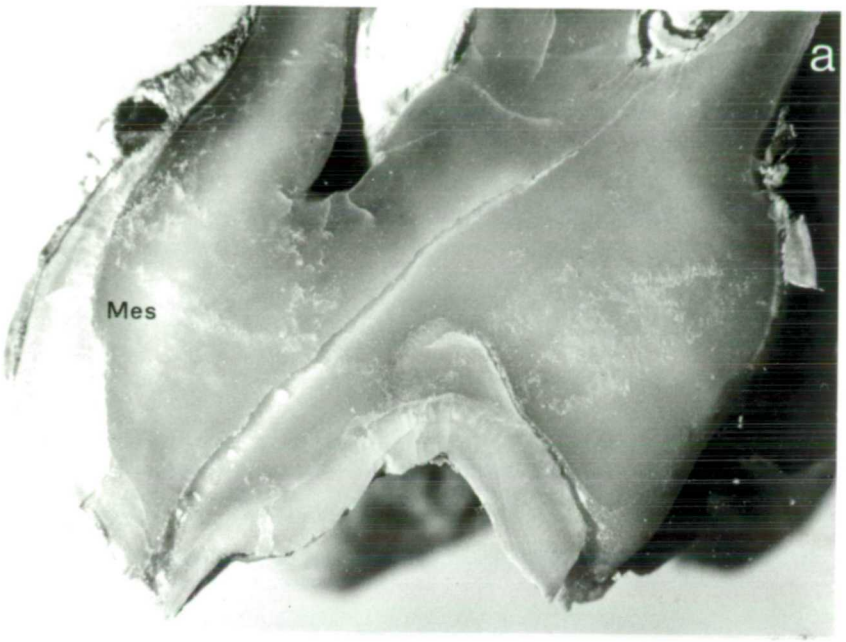
It was shown in the last section that at least a portion of the variation in any enamel thickness data will be the consequence of imperfect sectioning. The aim in this work was to devise a method which minimised these technical errors without requiring excessive material destruction, as would be involved for example in sampling sections at very short mesial-distal intervals which can only be achieved by serial grinding. As a result I decided to make a single saw cut which would expose two sections on which to make enamel thickness measurements. The saw cut involves the loss of a 350 μm slice of the tooth, which is considerably less than would be lost by Gantt's (1977) method which involves a minimum of two saw cuts as well as the removal of at least one slice of the tooth. The fact that the vertical enamel thickness measurements (f & g, Figure 4.2) are at or near a minimum on one or other of the two faces exposed by the primary cut (Figures 4.6 and 4.7) suggests that a single cut through the tips of the mesial cusps will be accurate enough to produce sections through the tips and maximum diameter of the dentine horns.

If the tips of the cusps are exactly coplanar with the maximum diameter of the dentine horns then a 350 μm wide cut will produce two faces each of which would be 175 μm, mesial and distal respectively, from the ideal midline position, assuming that the cut is perfectly through the cusp tips. If the maximum diameter of the dentine horns is displaced mesially or distally from the plane through the cusp tips then either the anterior or the posterior face exposed by the cut will

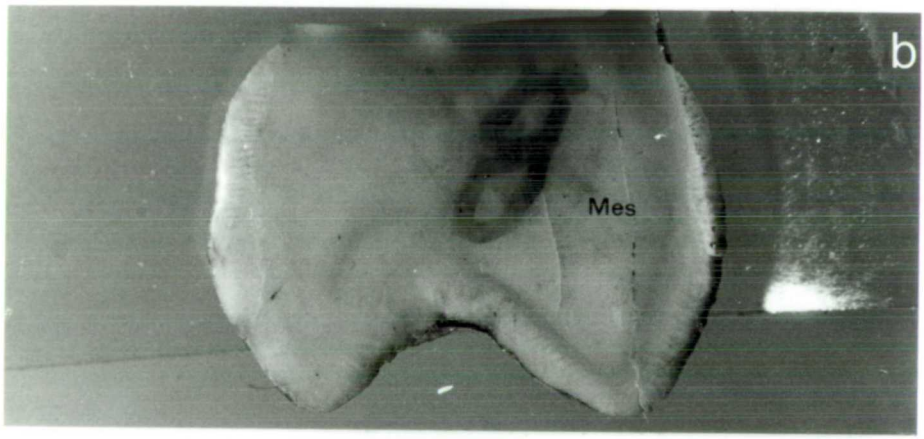
be closer to the true midline than would the other. Provided that the tips of the dentine horns do not deviate more than 350 μm mesially or distally from the plane through the cusp tips then one of the two faces must be within 175 μm of the position of the ideal plane of section.

A small sample of the teeth available for sectioning were therefore cut from mesial to distal through the buccal or the lingual cusps. Three of these sections are shown in Figure 4.10, these summarise what was found in all of the teeth sectioned in this plane (see Table 4.2). The tips of the dentine horns are usually just distal to the position of the tips of the cusps. Figure 4.10a shows a section in which the enamel does not make a clean edge with the dentine as the cut is lateral to the plane through the maximum diameter of the dentine horns so that small folds of enamel overlap the true position of the enamel-dentine junction exaggerating the enamel thickness. As a result of the relative opacity of the enamel the maximum diameter of the enamel-dentine junction can be seen through the enamel as a dark line on the photograph (this is even more apparent when viewed by light microscope). Thus when the saw cut has not passed exactly through the maximum diameter of the dentine horns, and therefore destroyed it, then this position may still be visible in one or other of the two sections. The position of the maximum diameter can be completely revealed by lightly polishing the section until the overlying layer of enamel is removed. When the overlying layer of enamel is thin then the enamel-dentine junction can be drawn onto a photograph of the section in the plane of the maximum diameter of the

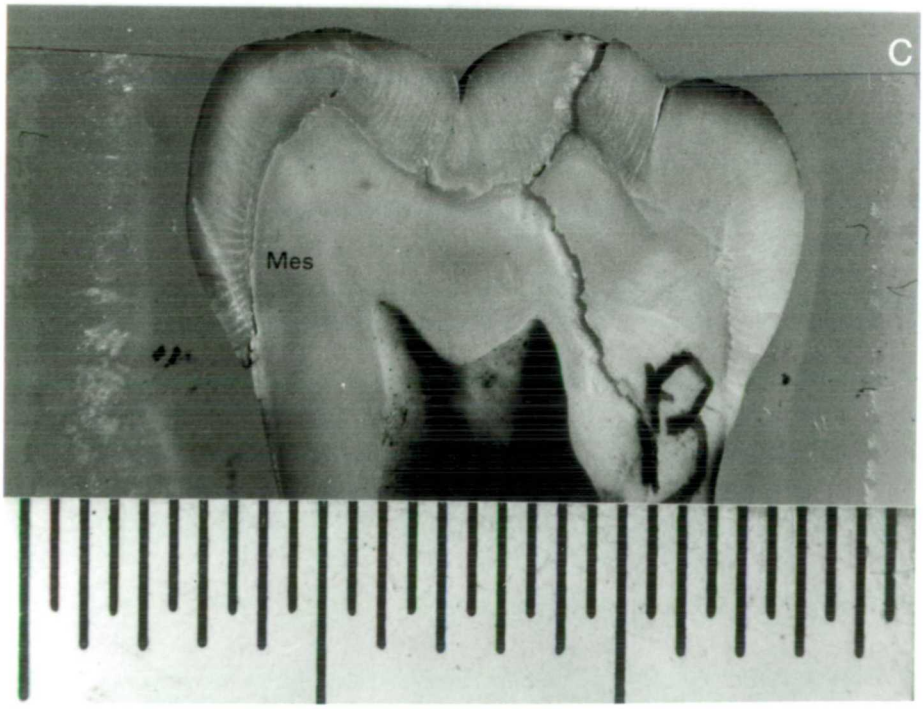
Figure 4.10: Mesial to distal sections through the buccal cusps.



G 14
M^2
Buc med.



Pa 13
M^1
Buc lat.



Ho 7
M_1
Buc lat.

dentine horns before measurements are taken.

The reasons why this should be considered as the true cross section have been discussed above and are shown diagramatically in Figures 4.8 and 4.9. The measurement which best describes enamel thickness is a radial measurement, this will always be the minimum dimension of the enamel thickness which can be measured (see Figures 4.8 and 4.9. Figure 4.10a shows how the thickness of enamel would have been exaggerated had the true position of the dentine horn maximum diameter not been superimposed for the purpose of measurement.

In the case of two cut faces neither of which show a layer of enamel overlying the true extent of the enamel-dentine junction this can only mean that the maximum diameter of the dentine horns has been destroyed by the cutting. In a few cases the enamel-dentine junction maximum diameter will have been exactly at the midline of the saw cut and both sections will reveal slightly exaggerated enamel thicknesses which will be metrically equal on the two faces. More usually one of the two cut faces will be closer to the midline than the other, this can be recognised as the one in which the minimum dimension of enamel thickness is exposed for any particular linear variable, as this is the less oblique section. The more closely the cut exposes the maximum diameter of the dentine horns the greater will be the measurements of the dentine and the lesser will be the enamel dimensions.

The aim, therefore, is to minimise measurements of enamel thickness while maximising measurements of the dentine in order to select the

value which is least influenced by obliquity of section (Figures 4.8 and 4.9). Measurements (a) - (e) (Figure 4.1) are all always selected from one of the faces as their measurement is interconnected. Generally the face which produces the greater value of dentine area ((b), Figure 4.1) also produces the lesser value for enamel cap area ((c), Figure 4.1) and is therefore the less oblique with regard to these variables. When the maximum diameter of the dentine horns has been destroyed (see Figures 4.11a-f, 4.12a,b, 4.14e-h and 4.15e-h) then the face which produces the maximum dentine area and the minimum enamel area cannot necessarily be used for the linear measurements ((f) - (p), Figure 4.2). Some measurements from both faces exposed by a saw cut are given in Table 4.5 and show that minimum, and therefore more nearly radial, measurements can only be achieved by combining data from the two faces when the maximum diameter of the dentine horns has been destroyed (G 13, Pa 16, Po 1 and Ho 8, Table 4.5). When the saw cut has passed just mesial or distal to the plane of the maximum diameter of the dentine horns (Figures 4.11g-l, 4.12c-j, 4.13a-k, 4.14a-d, i-l and 4.15a-d,i,j, then one of the cut faces can be selected to provide all of the enamel thickness measurements as in every case these are the lesser of the two values for each variable (see G 6 and G 11, Table 4.5).

The extent by which the two sets of measurements may vary when taken on faces only 350 μm apart in one tooth (Table 4.5) emphasises the necessity of the correction procedure employed here. This procedure means that the measurements presented in full in Appendix A and in summary Tables and Figures in this chapter are taken on sections which

are less than 175 μm away from the maximum diameter of the dentine horns. The worst situation which can arise, in terms of oblique sections exaggerating enamel thickness, is that the maximum diameter of the dentine horns is coplanar with the midline of the saw cut. In this situation the two faces are 175 μm away from the ideal plane and will give numerically identical values for each variable on either of the two faces, this situation was never encountered. A second possibility is that the maximum diameter of the dentine horns is destroyed but one or other of the two faces provides a truer section than the other, or data from the two faces is combined to approximate a "best section". When both faces provide an equal or nearly equal number of minimum values we may assume that the plane in which the values are measured is somewhat less than 175 μm removed from the ideal plane of section. The situation most commonly encountered is that the maximum diameter of the dentine horns is exposed or visible in one or other of the two faces in which case the measurements are taken at the ideal plane of section. I can see no way to improve the resolution of this method without involving the destruction of more tissue. However it is important to bear in mind the limits of resolution, i.e. that the data presented here can be shown to be within 175 μm of the ideal plane of section and are usually much closer than that.

4. Enamel Thickness

(a) Tooth Sections

A method was proposed above for recognising which face produced by a saw cut was the best for measuring enamel thickness. This method is based on the fact that it is impossible to produce a section in which the radial enamel thickness is underepresented (see discussion of oblique sections above). The measurements obtained for the two faces produced by a single saw cut for a number of specimens are shown in Table 4.5. The face on which the measurement is taken is identified as "mesial anterior" or "mesial posterior". Mesial refers to the fact that the cut passes through the mesial cusps, anterior means the section exposed on the anterior portion of the tooth which has been removed by the cut, posterior to the face revealed on the posterior portion of the tooth crown by the same cut. The identifications (G 13, Po 1 etc.) identify a particular tooth and thereby a specimen listed in Appendix A.

Representative tooth sections for each molar category for each species are shown in Figures 4.11 - 4.15. In some cases the two faces revealed by a single cut are shown, and for the modern taxa these are discussed in the Figure captions with reference to Table 4.5. Both cut faces of the fossil teeth sectioned are show in Figures 4.11 - 4.15 as these are most relevant to this work, as well as being the most interesting in their own right! A black spot indicates the buccal side of the tooth.

Figure 4.11: Buccal to lingual sections through the mesial cusps in maxillary first molars (M^1). A bla k spot indicates the buccal side of the tooth.

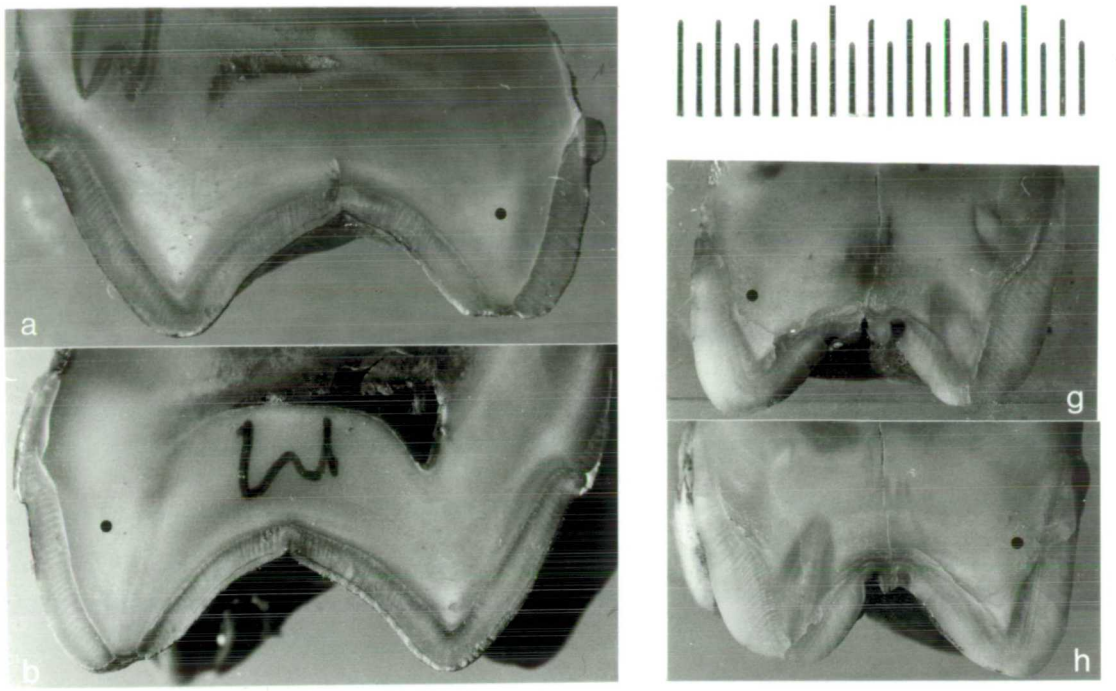
(a) Gorilla (G 13) mesial anterior face.
(b) Gorilla (G 13) mesial posterior face.
(c) Pan (Pa 16) mesial anterior face.
(d) Pan (Pa 16) mesial posterior face.
(e) Pongo (Po 1) mesial anterior face.
(f) Pongo (Po 1) mesial posterior face.
(g) Homo (Ho 16) mesial anterior face.
(h) Homo (Ho 16) mesial anterior face.
(i) Sivapithecus sivalensis (M 13365) mesial anterior face.
(j) S.sivalensis (M 13365) mesial posterior face.
(k) S.sivalensis (M 13366) mesial anterior face.
(l) S.sivalensis (M 13366) mesial posterior face.

The saw cut through the Gorilla M^1 has destroyed the maximum diameter of the dentine horns. The posterior face revealed by the cut shows small folds of enamel overlying the enamel-dentine junction on the lateral aspect of the buccal cusp, and this was corrected for the purposes of measurements. This situation is one in which data from both faces must be examined in order that minimum, and therefore radial, measurements are achieved (Table 4.5). The same situation is seen in the Pan M^1; in this case folds of enamel are visible on the lateral aspect of the lingual cusp on the anterior face. This suggests that the posterior face of the Pan section is closer to the maximum diameter of the dentine horns than is the anterior face. The measurements from the two faces are given in Table 4.5, measurements from the two faces must be taken and the minimum value for each variable selected (these values are underlined in Table 4.5). The saw cut through the Pongo M^1 has passed through the maximum diameter of the dentine horns (no folds of enamel are therefore visible nor any dark line revealing the true position of the maximum diameter of the dentine horns). The measurements for the two faces are given in Table 4.5. The mesial posterior face is closer to the true midline than is the mesial anterior face. This means that the enamel thickness measurements were taken in a plane less than 175 µm from the ideal plane of section.

The saw cut through the Homo M^1 has missed the maximum diameter of the dentine horns. The mesial anterior face is therefore showing obliquely sectioned enamel. The mesial posterior face is close to the true cross section although there is a small fold of enamel overlying the enamel-dentine junction on the lingual cusp. This was corrected for the purposes of measurement.

The saw cut through the mesial cusps of M 13365 has revealed the maximum diameter of the dentine horns on the mesial posterior face, and slight polishing of this face revealed a more oblique section. This face was therefore used for measurement and must lie at, or very close to, the ideal section plane. The cut through the mesial cusps of M 13366 has revealed the maximum diameter of the dentine horns on the mesial anterior face which was therefore used for measurement.

The mottled pattern in the dentine is seen as coloured zones on the original. These must reflect differences in the mineralization, but it has not yet been possible to establish how they may be correlated with structural features of the dentine. This will be attempted at a later date.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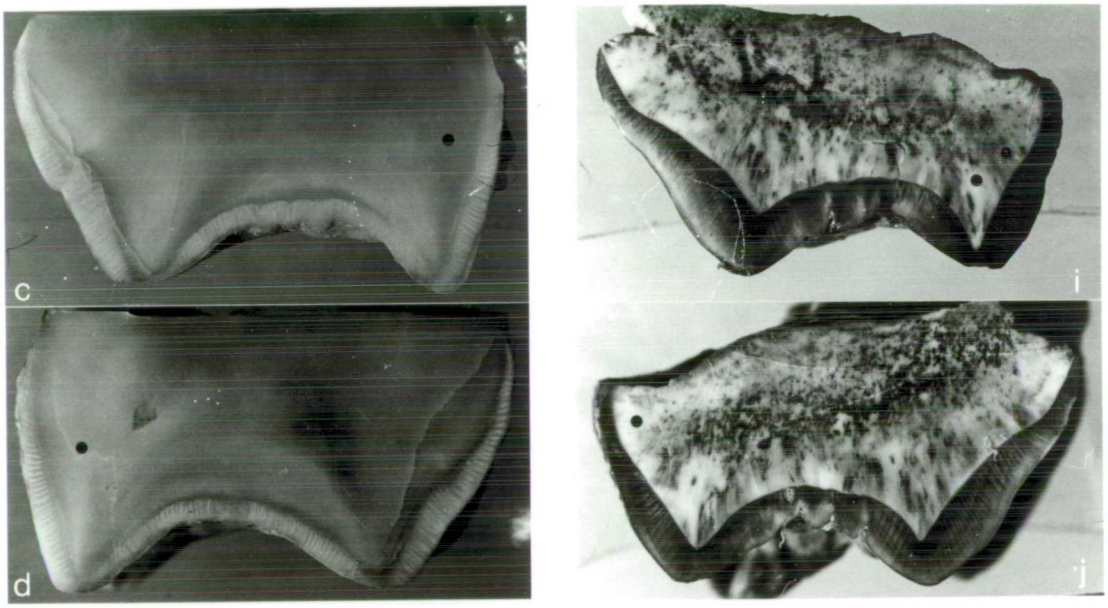
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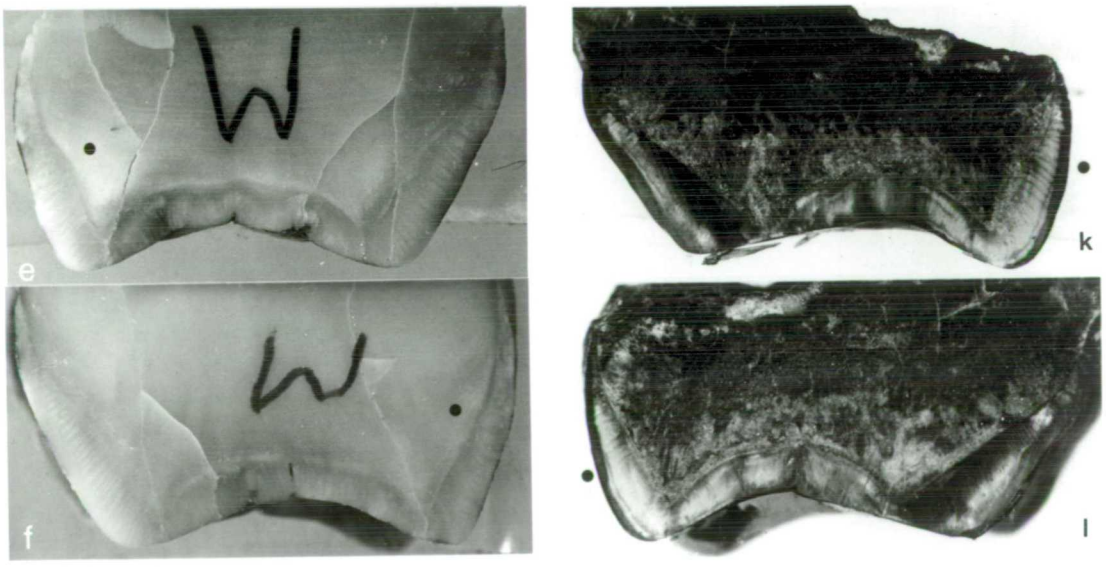
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Figure 4.12: Buccal to lingual sections through the mesial cusps in maxillary second molars (M^2).

(a) Gorilla (G 5) mesial anterior face.

(b) Gorilla (G 5) mesial posterior face.

(c) Pan (Pa 5) mesial anterior face.

(d) Pongo (Po 5) mesial anterior face.

(e) Pongo (Po 5) mesial posterior face.

(f) Homo (Ho 14) mesial posterior face.

(g) Sivapithecus alpani (BP 29) mesial anterior face.

(h) S.alpani (BP 29) mesial posterior face.

(i) S.darwini (BP 37) mesial anterior face.

(j) S.darwini (BP 37) mesial posterior face.

The saw cut through the Gorilla M^2 has not passed through the maximum diameter of the dentine horns although the cut is slightly oblique through the cusp tips. The mesial anterior face shows a very oblique section through the enamel on the lingual cusp and a slightly oblique section through the buccal cusp. The mesial posterior face shows the true position of the enamel-dentine junction for the lingual cusp but passes just distal to the maximum diameter of the dentine horn of the buccal cusp. The sections are combined to produce data for a near ideal cross section.

The cut through the mesial cusps of the Pan M^2 has revealed the maximum diameter of the dentine horns on the mesial anterior face which was used for measurement. The mesial posterior face was therefore 350 µm from the ideal plane of section and sectioned the enamel very obliquely.

The cut through the mesial cusps of the Pongo M^2 has just missed the maximum diameter of the dentine horns. The mesial anterior face shows an oblique section through the enamel especially on the lingual cusp. The mesial posterior face is close to the ideal plane of section but shows a small fold of enamel overlying the maximum diameter of the dentine horn on the lingual cusp. The true position is visible through the fold of enamel and was corrected for measurement. The saw cut through the mesial cusps of the Homo M^2 revealed the maximum diameter of the dentine horns in the mesial posterior face which was therefore used for measurement.

The saw cut through the mesial cusps of BP 29 has either passed through the maximum diameter of the dentine horns or has revealed it in the mesial posterior face. The mesial anterior face shows obliquely sectioned enamel and polishing of the mesial posterior face increased the apparent enamel thickness. The measurements from the mesial posterior face may be at the ideal plane of section or they may be slightly distal to it, but they can be no further than 175 µm away and are probably much closer. The section through the mesial cusps of BP 37 has passed very slightly mesial to the plane of the maximum diameter of the dentine horns. The mesial posterior face is at, or very close to the ideal plane of section.

A black spot indicates the buccal side of the tooth.

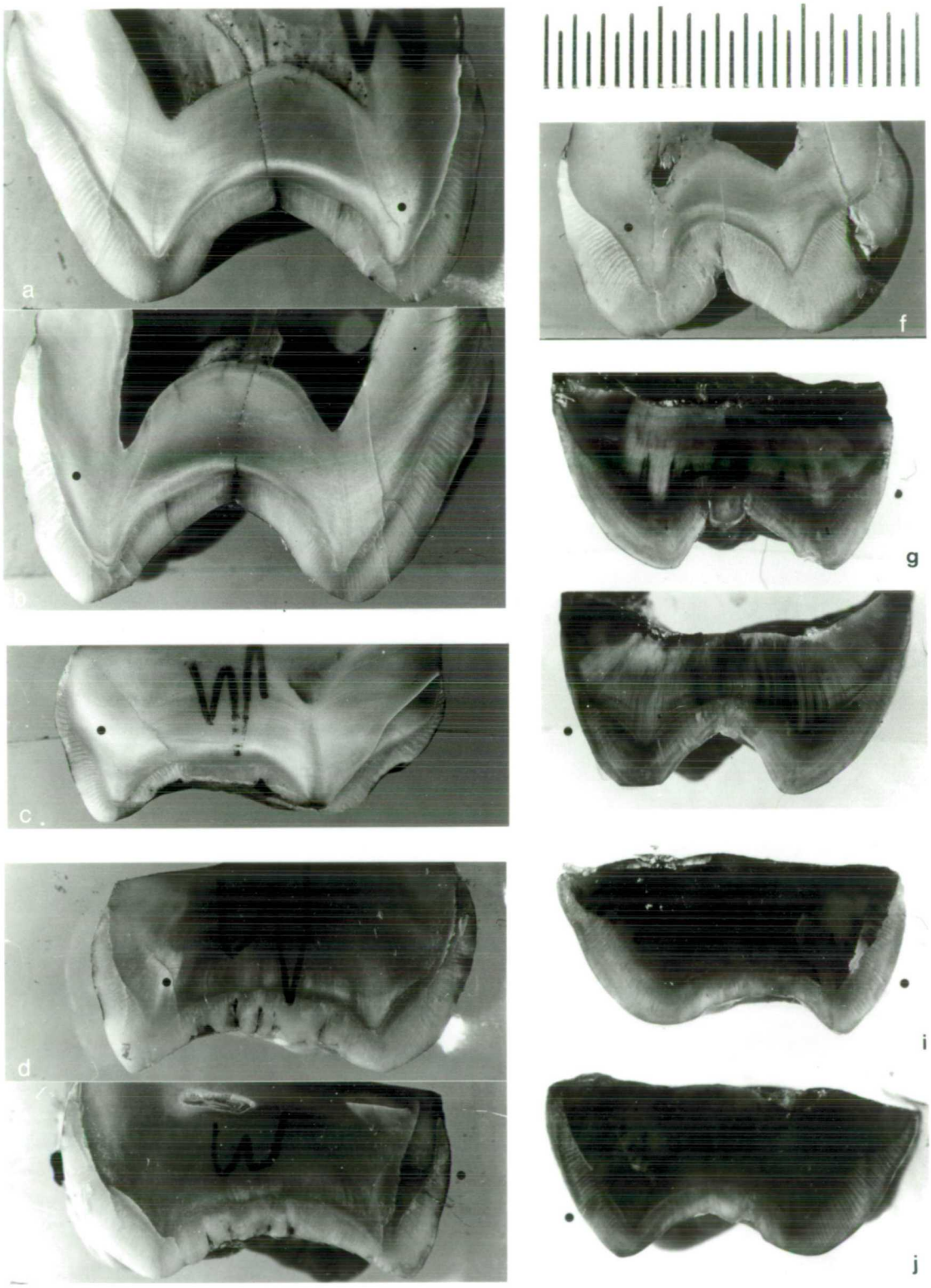
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Figure 4.13: Buccal to lingual sections through the mesial cusps of maxillary third molars (M^3) and mandibular first molars (M_1). A black spot indicates the buccal side of the tooth.

(a) Gorilla (G 6) mesial anterior face.
(b) Gorilla (G 6) mesial posterior face.
(c) Pongo (Po 18) mesial posterior fa e.
(d) Pan (Pa 6) mesial anterior face.
(e) Homo (ho 3) mesial posterior face.
(f) Gorilla (G 10) mesial anterior face (M_1).
(g) Pongo (Po 10) mesial anterior face (M_1).
(h) Pan (Pa 22) mesial posterior face (M_1).
(i) Homo (Ho 22) mesial posterior face (M_1).
(j) Sivapithecus alpani (BP 14) mesial anterior face (M_1).
(k) S.alpani (BP 14) mesial posterior face (M_1).

The saw cut through the Gorilla M^3 has passed mesial to the maximum diameter of the dentine horns. The mesial anterior face reveals a very oblique section through the enamel. The mesial posterior face also shows obliquely sectioned enamel, but in this case the true position of the maximum diameter of the dentine horns is visible through thin folds of enamel, and these were removed by light polishing to correct the photograph for measurement. The measurements from both faces are given in Table 4.5 and show that in a case where the maximum diameter of the dentine horns is not destroyed by the saw cut, only one face (in this case the mesial posterior) needs to be measured to obtain the best measurements of radial enamel thickness.

The saw cut through the mesial cusps of the Pongo M^3 revealed the maximum diameter of the dentine horns on the mesial posterior face with no folds of enamel overlying it. This face was therefore used for measurement, and is probably within a few microns of the ideal plane of section. The saw cut through the Pan M^3 revealed the maximum diameter of the dentine horns on the mesial posterior face, which was therefore used for measurement. The saw cut through the mesial cusps of the Homo M^3 passed slightly mesial to the maximum diameter of the dentine horns. The mesial posterior face is near to the ideal section with small folds of enamel overlying the enamel-dentine junction. This was corrected for the purpose of measurement.

The saw cut through the mesial cusps of the Gorilla M_1 passed just mesial to the maximum diameter of the dentine horns. The mesial posterior face shows a near ideal cross section with a fold of enamel overlying the enamel-dentine junction on the buccal cusp; thi- was corrected for measurement. The cut through the mesial cusps of the Pongo M_1 passed just distal to the maximum diameter of the dentine horns revealing a near ideal section on the mesial anterior face. The buccal cusp has been slightly worn, and its unworn condition was estimated for the purpose of measurement. The saw cut through the mesial cusps of the Pan M_1 passed just mesial to the maximum diameter of the dentine horns. The mesial posterior face is a near ideal with a small fold of enamel overlying the enamel-dentine junction on the lingual cusp; this was corrected for the purpose of measurement. The cut through the mesial cusps of the Homo M_1 passed mesial to the maximum diameter of the dentine horns so that the mesial posterior face is the better section. Small folds of enamel overlie the position of the enamel-dentine junction on the lingual cusp; this was corrected for measurement.

The saw cut through the mesial cusps of BP 14 has revealed the maximum diameter of the dentine horns on the mesial posterior face. The mesial anterior face shows an oblique section through the enamel cap and radial measurements cannot be taken on it. BP 14 is lightly worn and the unworn shape of the cusps was estimated for the purpose of measurement.

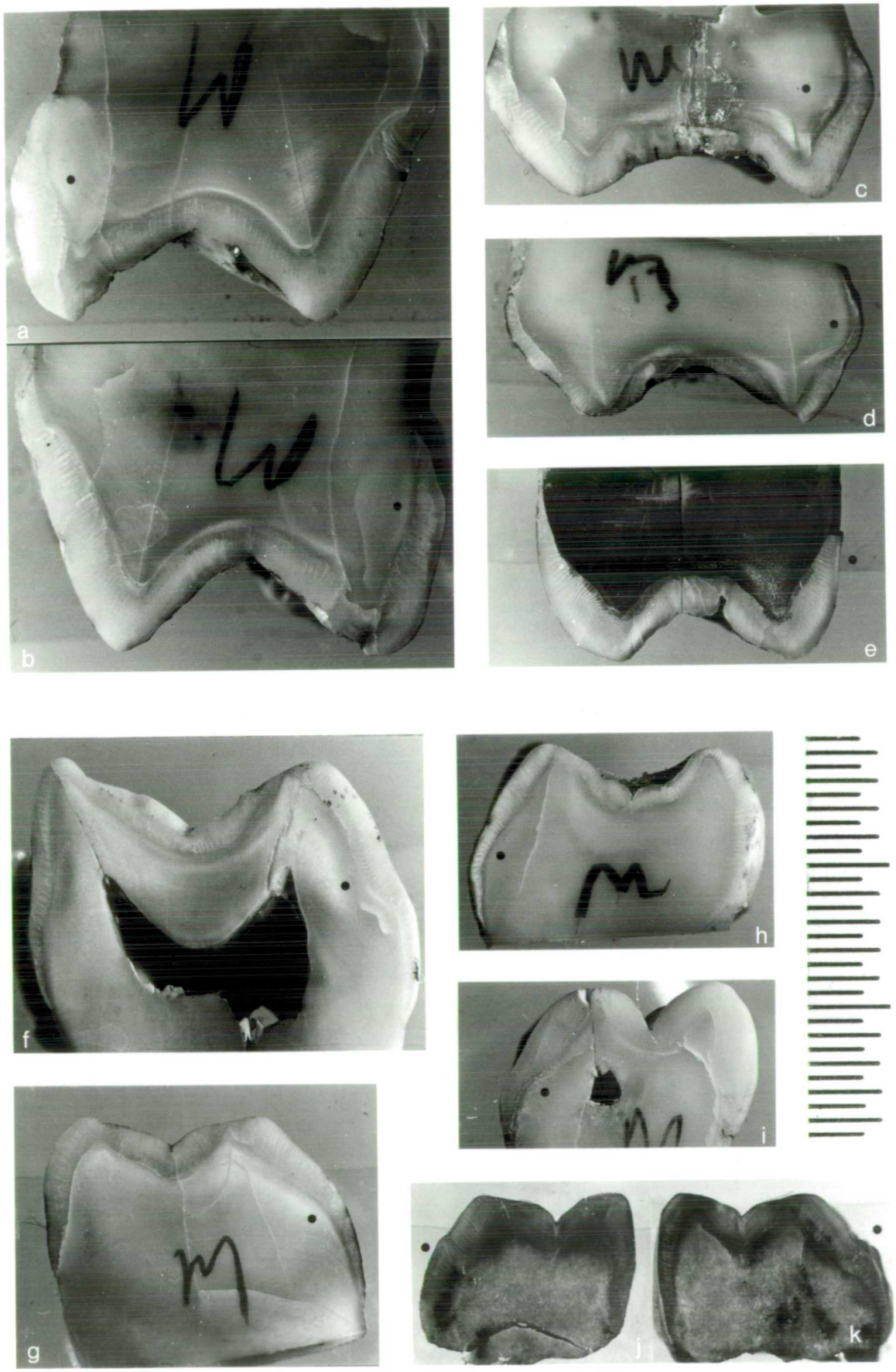
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Figure 4.14: Buccal to lingual sections through the mesial cusps of mandibular second molars (M_2).

(a) Gorilla (G 11) mesial anterior face.
(b) Gorilla (G 11) mesial posterior face.
(c) Pongo (Po 8) mesial posterior face.
(d) Pan (Pa 20) mesial anterior face.
(e) Homo (Ho 8) mesial anterior face.
(f) Homo (Ho 8) mesial posterior face.
(g) Sivapithecus alpani (BP 13) mesial anterior face.
(h) S.alpani (BP 13) mesial posterior face.
(i) S.alpani (BP 17) mesial anterior face.
(j) S.alpani (BP 17) mesial posterior face.
(k) S.darwini (BP 64) mesial anterior face.
(l) S.darwini (BP 64) mesial posterior face.

The saw cut through the mesial cusps of the Gorilla M_2 passed just mesial to the maximum diameter of the dentine horns. The mesial anterior face reveals a strongly oblique section through the enamel cap. The mesial posterior face also shows an oblique section through the enamel, but the maximum diameter of the dentine horns is preserved just distal to the plane of section. This face could therefore be corrected by lightly polishing the section until the maximum diameter of the dentine horns was exposed. This correction was made for the purpose of measurement; the measurements from both faces are given in Table 4.5. These show that when the maximum diameter of the dentine horns is not destroyed by the saw cut then one face (in this instance the mesial posterior face) can be used to provide the best estimates of radial enamel thickness for all of the variables.

The saw cut through the mesial cusps of the Pongo M_2 has passed slightly mesial to the maximum diameter of the dentine horns. The mesial posterior face is close to the ideal midline and when corrected to allow for the small fold of enamel over the enamel-dentine junction on the buccal cusp provides measurements at, or very close to, the ideal plane of section for radial measurements. The cut through the mesial cusps of the Pan M_2 passed just distal to the maximum diameter of the dentine horns. The mesial anterior face is therefore the better section for taking radial measurements. A small fold of enamel overlying the enamel-dentine junction on the buccal cusp was corrected for measurement.

The saw cut through the mesial cusps of the Homo M_2 has passed through the maximum diameter of the dentine horns. The measurements from both faces are given in Table 4.5 and indicate that the mesial posterior face is closer to the ideal midline than is the mesial anterior face although, as always when this situation has occured, measurements from both sections must be combined when the maximum diameter of the dentine horns has been destroyed by the saw cut.

The saw cut through the mesial cusps of BP 13 has passed through the maximum diameter of the dentine horns. The mesial posterior face is closer to the ideal plane of section than is the mesial anterior face. By combining data from the two faces a good estimate of radial enamel thickness is obtained.

The section through the mesial cusps of BP 17 has revealed the maximum diameter of the dentine horns on the mesial posterior face. The mesial anterior face shows an oblique section through the enamel cap. The cut through the mesial cusps of BP 64 has revealed the plane of the maximum dimension of the dentine horns, or a position just distal to it, on the mesial posterior face. The crown of BP 64 is slightly worn and allowance for this was made when taking the linear measurements.

A black spot indicates the buccal side of the tooth.

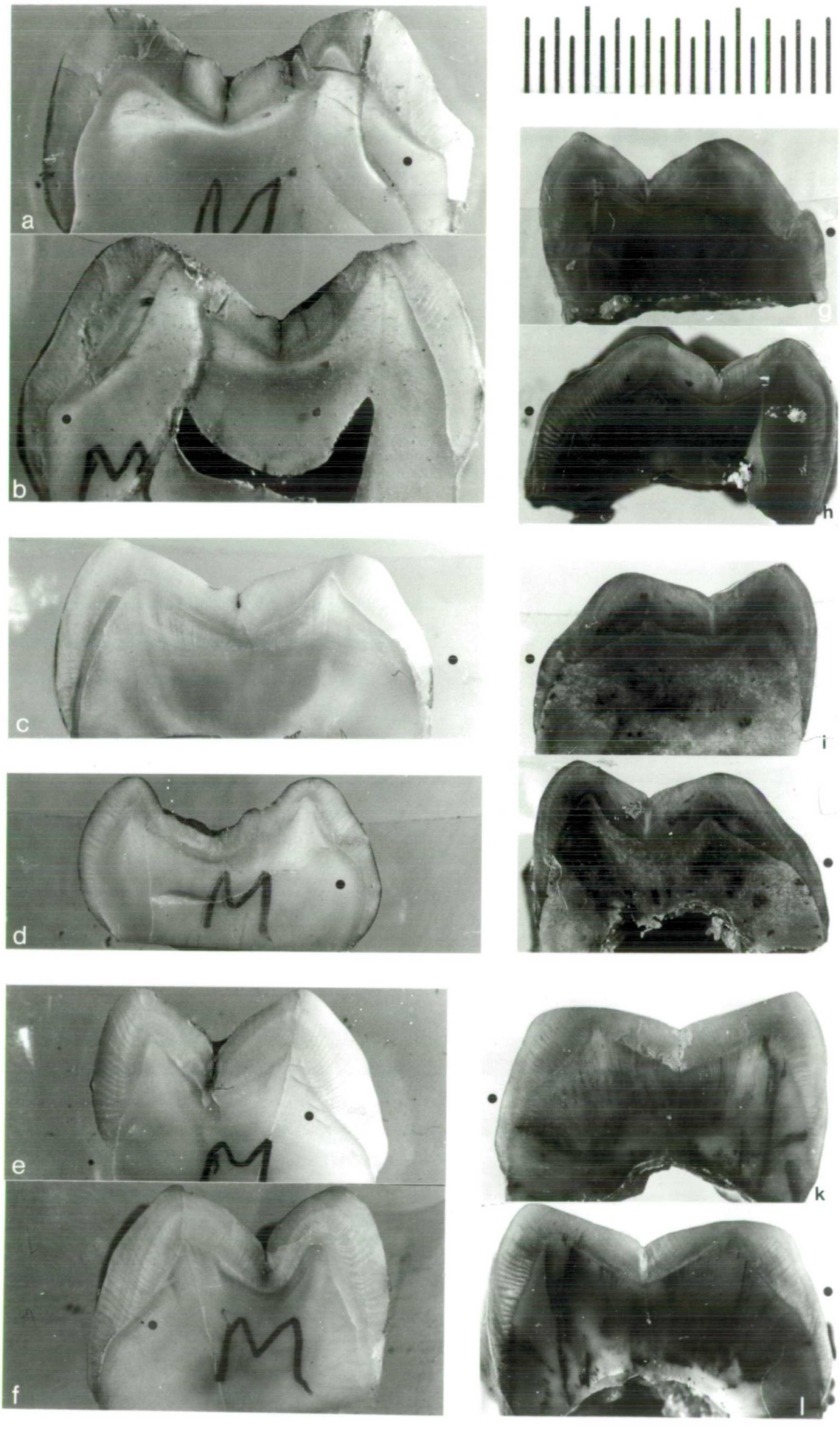
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Figure 4.15: Buccal to lingual sections through the mesial cu ps of mandibular third molars (M_3). A black spot indicates the buccal side of the tooth.

(a) Gorilla (G 21) mesial posterior face.

(b) Pongo (Po 9) mesial posterior face.

(c) Homo (Ho 24) mesial posterior face.

(d) Pan (Pa 12) mesial posterior face.

(e) Hylobates mesial anterior face.

(f) Hylobates mesial posterior face.

(g) Sivapithecus alpani (BP 12) mesial anterior face.

(h) S.alpani (BP 12) mesial posterior face.

(i) S.punjabicus (M 13367) mesial anterior face.

(j) S.punjabicus (M 13367) mesial posterior face.

(k) S.darwini (BP 4) mesial anterior face.

(l) S.darwini (BP 4) mesial posterior face.

The saw cut through the mesial cusps of the Gorilla M_3 has exposed the maximum diameter of the dentine horns on the mesial posterior face. The buccal cusp is worn and its estimated unworn condition was used for the purpose of measurement. The saw cut through the mesial cusps of the Pongo M_3 passed slightly mesial to the midline of the dentine horns. The small folds of enamel seen on the lingual cusp were corrected for prior to measurement. The section through the mesial cusps of the Homo M_3 passed slightly mesial to the maximum diameter of the dentine horns. Small folds of enamel can be seen on the buccal cusp overlying the enamel-dentine junction; these were corrected for the measurements. The saw cut through the mesial cusps of the Pan M_3 has similarly exposed the maximum diameter of the dentine horns on the mesial posterior face. Again the wear was allowed for in taking the linear measurements. The saw cut through the mesial cusps of the Hylobates M_3 has exposed the maximum diameter of the dentine horns on the mesial posterior face; this was used for the measurements in Table 4.26.

The saw cut through the mesial cusps of BP 12 has passed through the maximum diameter of the dentine horns, but obliquely so that a true section has not been obtained. The measurements for the lingual cusp are reasonable estimates of the radial thickness but the buccal cusp has not been properly sectioned, and for this reason the average enamel thickness (c/e, see Figure 4.1) was not calculated. The saw cut through the mesial cusps of M 13367 passed through the maximum diameter of the dentine horns. The mesial anterior face provides the best, most nearly radial, section through the enamel and was used for measurements (a) - (e) (see Figure 4.1) but measurements from both faces were combined for the linear measurements. The section through the mesial cusps of BP 4 has revealed the maximum diameter of the dentine horns on the mesial anterior face and this face was therefore used for measurement.

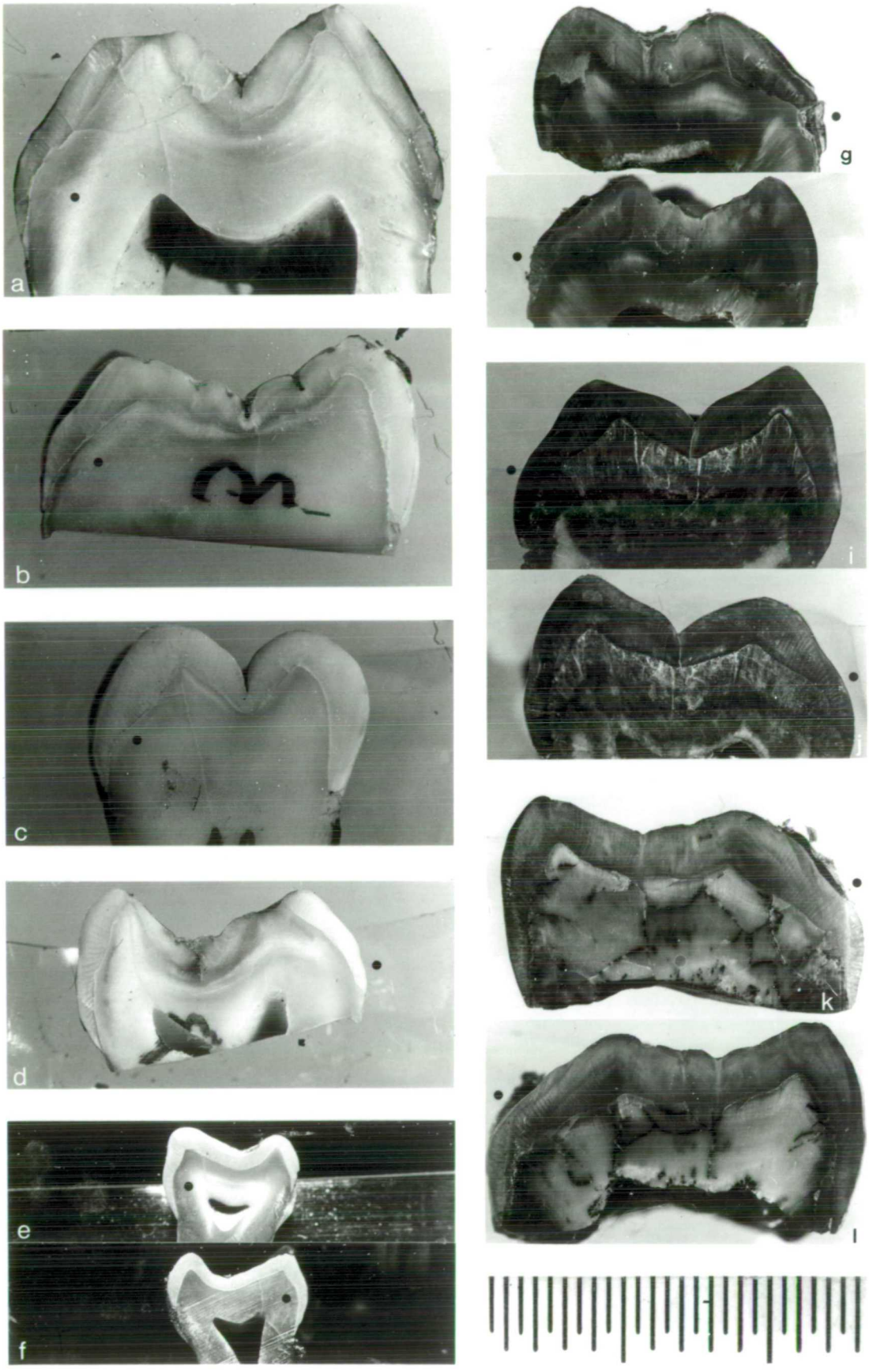
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Table 4.5: Enamel thickness measurements taken n the two faces revealed by a saw cut

I.D.	a	b	c	d	e	f	g	h	i	j	k	l	m	n
G 13 mes ant	72.0	55.3	16.7	26.2	24.5	0.71	0.47	0.77	0.71	0.71	1.00	0.83	1.09	0.83
G 13 mes.post	91.2	71.0	20.2	28.8	26.8	1.00	0.35	0.94	0.71	0.77	0.88	0.73	0.94	0.74
Pa 16 mes.ant.	67.1	54.1	13.0	23.9	22.2	0.53	0.24	0.40	0.54	0.53	0.64	0.83	0.66	0.93
Pa 16 mes post	66.5	54.9	11.6	25.7	22.3	0.41	0.24	0.55	0.50	0.59	0.68	0.70	0.68	1.04
Po 1 mes ant	66.6	47.3	19.3	22.7	19.4	1.02	0.98	0.98	0.98	1.06	1.25	1.23	1.30	1.38
Po 1 mes post	70.9	53.7	17.2	23.1	20.8	0.85	0.71	0.86	1.01	0.88	1.01	1.17	1.09	1.30
Ho 8 mes ant	45.6	21.7	23.9	20.4	14.8	1.89	1.59	1.65	1.30	1.18	1.79	1.37	1.89	1.37
Ho 8 mes post	50.4	27.0	23.4	21.2	15.9	1.77	1.53	1.41	1.27	1.42	1.79	1.10	1.86	1.10
G 11 mes ant	93.5	61.1	32.4	28.5	23.4	1.18	1.59	1.36	1.42	1.24	1.46	1.25	1.95	1.26
G 11 mes post	103.7	76.5	27.2	29.9	26.9	0.59	0.71	1.06	0.83	1.06	1.32	1.01	1.53	1.03
G 6 mes ant	-	-	-	-	-	2.24	2.48	1.30	1.36	1.18	1.59	1.89	1.65	2.12
G 6 mes post	110.2	85.5	24.7	32.2	28.4	0.83	1.53	0.85	1 06	0.65	0.88	1.06	0.88	1.12

Notes: I.D. = identification of tooth (see Appandix A), mes ant = mesial anterior face, mes post = mesial posterior face.

(a) - (n) are enamel thickness measurements as shown in Figures 4.1 and 4.2.

Underlined figures are those used as results for the "best section" when the maximum diameter of the dentine horns has been destroyed.

(b) Scaling

It seems a reasonable assumption that any aspect of the enamel thickness would increase with tooth size, and therefore body size. Gantt (1977) and Kay (1981) have shown that across a range of catarrhines enamel thickness does increase as the animals become larger. This suggests that some kind of scaling factor should be incorporated in a measurement of enamel thickness. It is undesirable to employ any crown dimensions as scaling factors, as was done by Kay (1981), because dimensions such as crown length contain a component equal to two times the enamel thickness in the plane of measurement, and it is therefore not in any way an independent variable. Thus it would seem more logical to use some measurement of the pulp, dentine or cementum, or a combination of these, as a scaling factor as these are likely to be more independent variables.

The factors which actually determine the enamel thickness, in terms of cell and developmental biology, are the rate at which enamel formation takes place and the period of time during which the enamel of a particular tooth forms. One potential way to scale enamel thickness measurements would be with reference to their developmental period, effectively a mean daily formation rate. The method involves considerable technical difficulty and is not yet sufficiently developed to be uniformly used, but it does offer a realistic way to compare enamel thickness between species on the basis of well understood cellular processes (see Chapter 5).

In the present work, several tooth crown dimensions which exclude the

contribution of enamel thickness have been examined for their utility as scaling factors. These include cervical length and area, the area of material (dentine and pulp) contained below the enamel-dentine junction (measurement (b), Figure 4.1) and a straight line connecting the cervical ends of the enamel-dentine junction, and the length of the enamel-dentine junction.

It has been suggested that scaling factors are significant when making inter specific comparisons of enamel thicknesses (Gantt, 1977; Kay, 1981) but the question of intra specific scaling factors have not previously been addressed. There are no a priori reasons to suppose that a large individual should have thicker enamel on, for example M_1, than a small individual of the same species. The reason for this is that the tooth forms from the inside outwards so that the enamel-dentine junction is defined during tooth formation before the enamel is formed. The size of the enamel-dentine junction determines the number of ameloblasts which are available to form the enamel and therefore the intrinsic size of the tooth. The size of the completed crown depends on the distance which is travelled by each ameloblast during its passage from the enamel-dentine junction to the tooth surface, as no ameloblasts are formed other than at the enamel-dentine junction, and there is no reason to suppose that the ameloblasts of a large individual would produce enamel more quickly than the ameloblasts of a smaller individual of the same species. There is some evidence that the rate of enamel formation is related to the prism packing type and varies only when the prism type changes or in cases of gross developmental defects such as hypoplasia

(Boyde and Martin 1982, 1983; see also Chapter 5). The only other possible reason that large individuals should have thicker enamel than smaller individuals of the same species would be if the developmental period is longer in large individuals. There is, presently, no evidence to support this assumption. There are therefore no a priori reasons to assume that intra specific scaling factors will be significant. The empirical evidence relating to this question is discussed below.

(c) Enamel thickness variation in different tooth classes

The influence of developmental period on enamel thickness raises a potential problem in combining enamel thickness data for different tooth classes as each molar tooth may develop over a different period. This cannot be evaluated on the basis of eruption dates as enamel formation may not be continuous from the time of initial tooth germ formation until eruption. In humans the third molars are fully formed a long time before they erupt. No evidence is yet available to say whether enamel forms for different periods for different molar tooth types. At present this possibility can only be addressed by examination of completed enamel thickness in different molar teeth of single individuals. A proposal of a method to directly address this question is made in Chapter 5.

A number of individuals provided associated teeth for enamel thickness measurements. Those from which three or more teeth were sectioned from buccal to lingual are shown in Table 4.6 with their average enamel thickness measurements (c/e, see Figure 4.1).

Table 4.6: Average enamel thickness (c/e, Figure 4.1) in individuals providing three or more teeth.

Genus	Museum number	M^1	M^2	M^3	M_1	M_2	M_3	Range	Mean
Pan	M 1939.3373	-	-	-	0.60+	0.61	0.46+	0.15?	0.56+
Pan	M 1939.3387	0.52+	0.67	-	0.59+	0.74	-	0.22?	0.63+
Gorilla	M 1857.11.2.2	0.90+	0.93	-	0.89	-	-	0.04	0.91+
Gorilla	M 1939.940	-	0.83	0.87	-	1.01	1.05	0.22	0.94
Gorilla	M 1979.1322	-	0.81	0.84	-	0.73	-	0.11	0.79
Homo	M 4.5217	-	-	-	0.92	1.40	1.30	0.48	1.21
Homo	M 4.5440	0.98	0.82+	1.12	-	-	-	0.30?	0.97+
Pongo	M 1976.1435	-	1.13	-	-	1.08+	0.98	0.15	1.06+
Pongo	M 1976.1439	0.83	-	-	0.94+	1.08+	-	0.25+	0.95+
Pongo	M 1976.1441	1.02+	1.07	-	-	1.00+	1.17	0.17?	1.07+
Pongo	M 1976.1444	1.05	1.19	1.24	0.89+	-	1.36	0.47?	1.15+

Notes: Museum number gives the listing of the specimen in the British Museum (Natural History) catalogue.

Range = the range of average enamel thickness (c/e, Figure 4.1) values found in the molars of one individual.

Mean = the mean value of average enamel thickness (c/e, Figure 4.1) for each individual.

+ = value slightly reduced by wear.

? = range of values increased by wear reduced minimum.

The data in Table 4.6 show a trend which suggests that enamel thickness increases from anterior to posterior teeth, although a number of individuals have somewhat reduced enamel thicknesses in third molars. It would be desirable to remove any variability in enamel thickness measurements between different teeth from one individual which could be accounted for by differences in tooth size. However, it is found that none of the dimensions of tooth size studied follow similar trend in size changes to enamel thickness. Figure 4.16 shows diagramatically the change in a number of variables from tooth to tooth in one individual which provided the greatest number of tooth samples. None of these measurements of tooth size follows the same pattern as changes in enamel thickness although crown breadth across the mesial cusps shows a similar pattern. Crown breadth contains an element of enamel thickness and is therefore inappropriate as a scaling factor. The use of any of the tooth size measurements which are independant of enamel thickness increases the range of variability for a single individual. The samples are not large enough to support any definite statements regarding differences in enamel thickness between upper and lower molars but do indicate that enamel thickness tends to be greater on posterior molars. This trend may be related to differences in the developmental period between these teeth although that hypothesis cannot be tested at present.

The main issue with regard to the data in Table 4.6 is whether it is justifiable to combine enamel thickness measurements from different molar teeth in order to provide a statistically useful sample of data which can be compared between species. Table 4.7 shows the range of

values of average enamel thickness (c/e, Figure 4.1) for the small samples of teeth of each molar type. By comparing the range of average enamel thickness (c/e) values in one individual with the range of c/e values in each molar tooth type it is possible to assess the effect of combining data from different molar types. The range of average enamel thickness (c/e, Figure 4.1) values for the different teeth in one individual is identical to the range for one tooth in several individuals. The only apparent exception is one individual of Pongo pygmaeus (M 1976.1444) but this can probably be discounted as a result of the low average enamel thickness (c/e) value for M_1 which is considerably reduced as a result of the tooth being worn. It should also be noted that the ranges of (c/e) values are, predictably, greater when the sample size is increased. The samples in each case are very small but they do at least indicate that the mean enamel thickness (c/e) data are no more variable across all molar types within one individual than they are within one tooth type which combines data from several individuals. It is certainly justifiable to combine data from all molar teeth from one species on a priori grounds as the effect can only be to increase the range of variation of the enamel thickness data for the species.

The fact that enamel thickness measurements are quite different in teeth from one individual (Figure 4.16) implies that a considerable portion of the intra-specific variability will not be explainable by body size or tooth size. This is by definition the case for teeth from a single individual.

Table 4.7: Average enamel thickness (c/e, Figure 4.1) by molar tooth type

Genus		M^1	M^2	M^3	M_1	M_2	M_3
Pan	n	2	3	1	3	4	1
	Mean	0.49+	0.64	0.47+	0.63	0.68	0.46+
	Min	0.46+	0.53+	-	0.59+	0.61	-
	Max	0.52+	0.71	-	0.70	0.74	-
	Range	0.06	0.18?	-	0.11?	0.13	-
Gorilla	n	3	3	3	2	4	2
	Mean	0.81	0.86	0.85	0.76	0.96	0.99
	Min	0.75	0.81	0.83	0.62+	0.73	0.93+
	Max	0.90	0.93	0.87	0.89	1.13	1.05
	Range	0.15	0.12	0.04	0.27?	0.40	0.12?
Homo	n	2	2	3	2	2	2
	Mean	1.22	1.31	1.09	0.85	1.44	1.26
	Min	0.98	0.82+	1.01	0.78+	1.40	1.21
	Max	1.45	1.80	1.15	0.92	1.47	1.30
	Range	0.47	0.98?	0.14	0.14?	0.07	0.09
Pongo	n	3	3	2	3	3	3
	Mean	0.97	1.13	1.22	0.95	1.05+	1.17
	Min	0.83	1.07	1.19	0.89+	1.00+	0.98
	Max	1.05	1.19	1.24	1.02	1.08+	1.36
	Range	0.22	0.12	0.05	0.13?	0.08	0.38

Notes: n = number of teeth sampled
Min = minimum value found, Max = maximum value found
Range = difference between minimum and maximum
+ = value slightly reduced by wear
? = range increased by wear reduced minimum

Figure 4.16: Tooth dimensions in one individual of Pongo pygmaeus (M 1976.1444).

Plot 1: shows average enamel thickness (c/e, Figure 4.1) (mm)

Plot 2: shows dentine area (b, Figure 4.1) (mm^2)

Plot 3: shows mesial-distal root length multiplied by the cervical breadth of the mesial root (MDR x BLR) (mm^2)

Plot 4: shows mesial-distal crown length multiplied by the crown breadth across the mesial cusps (MDC x BLC) (mm^2)

Plot 5: shows the cervical breadth of the mesial root (BLR) (mm)

Plot 6: shows crown breadth across the mesial cusps (BLC) (mm)

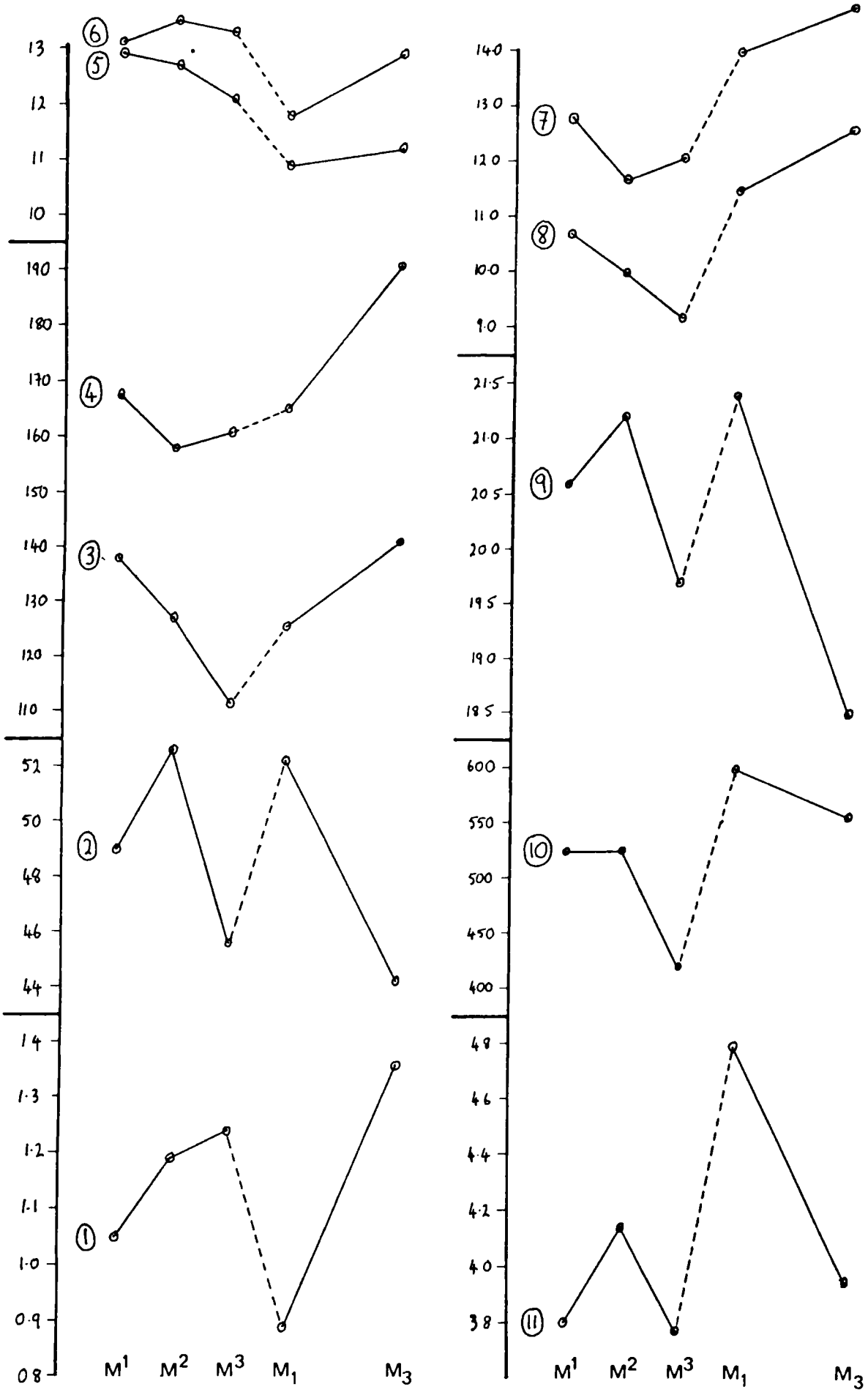
Plot 7: shows mesial-distal crown length (MDC) (mm)

Plot 8: shows mesial-distal root length (MDR) (mm)

Plot 9: shows enamel-dentine junction length (e, Figure 4.1) (mm)

Plot 10: shows the product of dentine area (b, Figure 4.1) and mesial-distal root length (MDR) (mm^3)

Plot 11: shows average height of the dentine, dentine area (b, Figure 4.1) divided by the cervical breadth of the mesial root (BLR) (mm)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19·0
18·5
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(d) Dental estimators of body weight

Since body weight data are not available for the individual specimens sampled here some measurement of tooth size must be used in any attempt to scale enamel thickness measurements with regard to both intra and inter-specific variation. I have suggested that crown dimensions cannot be considered as independant variables with regard to enamel thickness because a portion of their magnitude is directly accounted for by enamel thickness. Data for tooth dimensions which do not contain an element of enamel thickness have not been previously assessed for their relationships with body size. The data presented here samples only a small number of species so regression equations cannot be calculated or correlation coefficients compared with any confidence (Dr. Michael Hills, personal communication). The purpose of this analysis was to select a measure of tooth size which does not include any enamel component but which appears to be related to body size. This is best achieved by inspection of plots of dental variables against body weight (Hills, personal communication). In order to provide a useful dimension for scaling enamel thickness it is necessary that the variable appears to increase with body size and also to provide clear separation of the species sampled on the y-axis, which will subsequently be used as a size measurement (Hills, personal communication). The data which I have used are for combined samples of molar teeth. Body weights were the average of the male and female means for each species and were provided by Dr. Ben Rudder. The plots of a number of dental variables against body weight are shown in Figure 4.17. The archaeological Homo sapiens sample was treated as a

fossil sample for this purpose as the body weight cannot be assumed to be equal to that of modern humans. In addition it seems probable that grade differences exist between tooth size in the great apes and in Homo sapiens in that cultural influences appear to have resulted in humans being microdont.

The plots in Figure 4.17a and 4.17b show the mesial to distal length of the crown and the cervix respectively. By inspection the measurement of crown size which excludes enamel (i.e. the cervix length) seems to reflect size differences in a similar way to crown dimensions and on a priori grounds is more appropriate for use in scaling enamel thickness measurements as it contains no enamel component. The same pattern is seen in Figure 4.17c and 4.17d which compare tooth crown area with tooth cervix area. In these four plots the dental variable does increase with size with Pongo apparently having relatively large teeth for its body weight, or Gorilla having relatively small teeth for its size. The plot in Figure 4.17e shows the relationship between dentine area (b, Figure 4.1) and body weight. This variable increases with size for the species sampled and provides good separation on the y-axis. It has the advantage that it is measured in the same way as the enamel thickness measurements (i.e. from scaled photographs) and that the relationship with size is more linear than is the case for the cervical dimensions for the species sampled. The plot in Figure 4.17f shows average dentine height (dentine area/ cervical breadth across the mesial cusps, b/B-LR, Figure 4.1) against body weight. The relationship is nearly linear but provides poor separation on the y-axis. Interestingly

Pongo appears to have a relatively small average dentine height despite its having an apparently large cervical area. The samples presented here are too small to provide clear answers with regard to this but it is suggestive that the dentine portion of crown height is relatively small in Pongo. This proposition is examined in more detail in the light of measurements of dentine horn height below. The plot in Figure 4.17g shows enamel-dentine junction length against body weight. The relationship appears to be reasonably linear but since enamel-dentine junction length is used to compute average enamel thickness (c/e, Figure 4.1) its use as a dental estimate of body weight is inappropriate. The length of the enamel-dentine junction in Pongo appears to be relativlely less than in the African apes. This further suggests that the enamel-dentine junction is relatively flat in this taxon as the area of tissue below the enamel-dentine junction (b, Figure 4.1) does not show this.

The final plot in Figure 4.17h shows average enamel thickness (c/e, Figure 4.1) against body weight. There is no linear relationship with size for this variable. The position for Homo is shown assuming modern body weight, although this assumption is recognised to be invalid, it shows however that even assuming modern body weight human enamel is relatively thick especially when it is considered that the body weight is almost certainly a maximum value compared to archaeological Homo sapiens.

It would of course be possible to produce a relative enamel thickness measurement using body weight (or the cube root of body weight) but

this would mean that results for fossil species could not be included. The purpose of this analysis is to assess enamel thickness in fossil species, as well as the significance of enamel thickness in hominoid evolution, so this course is inappropriate. Of the dentine variables examined here dentine area (b, Figure 4.1) seems to be the most suitable as it shows a nearly linear relationship with body size for the sample for which data are available and separates the species clearly on the y-axis and has the advantage that it is measured in the same way as the enamel thickness measurements. This measurement of size will therefore be used as the primary scaling factor.

The average enamel thickness (c/e, see Figure 4.1) is considered on a priori grounds to be the best description of enamel thickness in the plane of section, this supposition is evaluated below. A number of the indirect measurements of body size were tested for their ability to explain intra-specific differences in average enamel thickness (c/e) for the sample data (see Tables 4.8 - 4.11).

Figure 4.17: Log_{10}/log_{10} plots showing dental size against body weight. The dental size measurements are as follows:

a) Mesial to distal crown length. (mm)

) Mesial to distal length of the cervix. (mm)

c) Mesial to distal crown length x buccal to lingual crown breadth. (mm^2)

d) Mesial to distal length of the cervix x buccal to lingual breadth of the cervix across the mesial cusps. (mm^2)

e) Dentine area (b, Figure 4.1). (mm^2)

f) Dentine area/the buccal to lingual breadth across the cervix of the mesial cusps. (mm)

g) Enamel-dentine junction length (e, Figure 4.1). (mm)

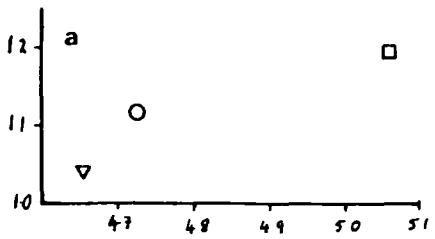
h) Average enamel thickness (c/e, Figure 4.1). (mm)

The symbols are as follows: ▽ = Pan

□ = Gorilla

☼ = Homo

○ = Pongo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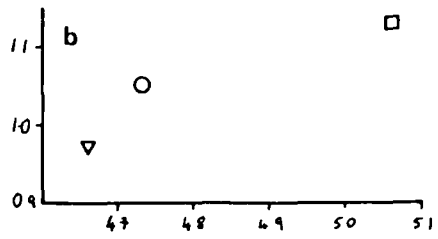
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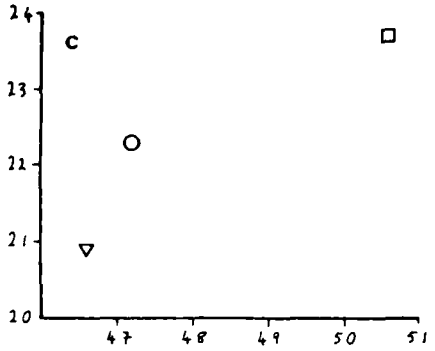
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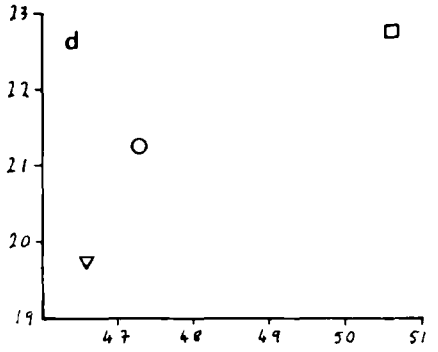
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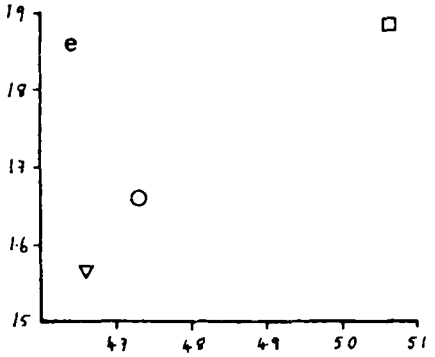
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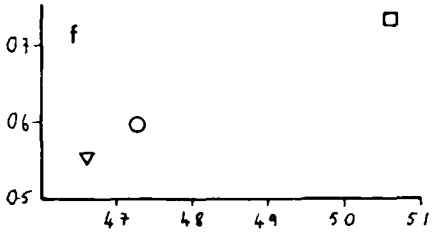
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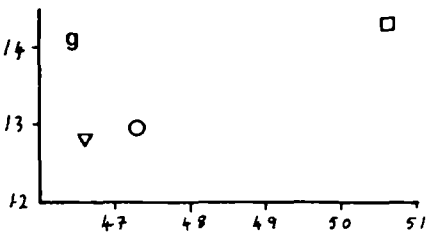
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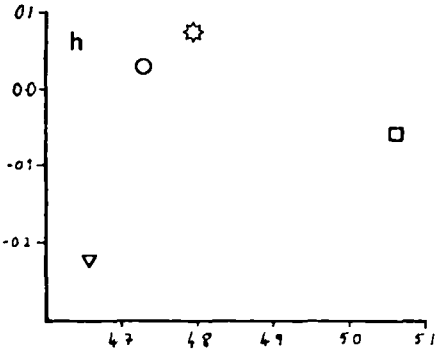
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(e) Enamel thickness in relation to size

Tooth crown length has been used to scale enamel thickness measurements between species (Kay, 1981). Gingerich et al (1982) suggested that the crown area (M-D x B-L) is more highly correlated with body size, and its use seems more appropriate when both upper and lower molars are being considered. These crown measurements are always, with the exception of Pongo crown area, more highly correlated with average enamel thickness than are the same measurements taken at the cervix (Tables 4.8 - 4.11). I have suggested above that crown dimensions should not be considered to be independant variables for comparison with enamel thickness measurements because the dimensions include an element of enamel thickness and these higher correlations confirm the fallacy of such an assumption.

With crown dimensions excluded I have examined a number of variables relating to the amount of dentine, pulp and cementum on a tooth. The significance level values given in Tables 4.8 - 4.11 may be used to assess how significant the correlation is. Anything less than 95% certainty was immediately excluded as not significant (Simpson, Roe and Lewontin, 1960). When these poor correlations are excluded, as well as the crown measurements, Pan and Gorilla have only cervical length remaining. No good correlations were found for Homo or Pongo. This means that no clear correlation can be established between enamel thickness and tooth size, when measured to exclude the contribution of the enamel cap, and this result applies to each of the species sampled here. This tends to confirm the assumption, made on a priori grounds

from knowledge of enamel development and data from several teeth from one individual, that intra-specific differences in enamel thickness cannot be simply explained as the result of body size differences. Therefore raw data can be used for within species purposes.

Table 4.8: Regression values for $\log_{10}$average enamel thickness (c/e, Figure 4.1) on $\log_{10}$variable in Pan

Variable	n	r	sig level	r^2
M-D crown length	14	0.698	99%	49%
M-D cervix length	14	0.563	95%	32%
M-D x B-L crown	14	0.404	n.s.	16%
M-D x B-L cervix	14	0.094	n.s.	1%
EDJ length (e, Figure 4.1)	14	-0.083	n.s.	1%
Dentine area (b, Figure 4.1)	14	-0.115	n.s.	1%
b x M-D cervix	14	0.141	n.s.	2%
b/B-L cervix	14	0.144	n.s.	2%

Table 4.9: Regression values for $\log_{10}$average enamel thickness (c/e, Figure 4.1) on $\log_{10}$variable in Gorilla

Variable	n	r	sig level	r^2
M-D crown length	16	0.711	99%	51%
M-D cervix length	16	0.520	95%	27%
M-D x B-L crown	17	0.596	98%	36%
M-D x B-L cervix	17	0.265	n.s.	7%
EDJ length (e, Figure 4.1)	17	-0.159	n.s.	3%
Dentine area (b, Figure 4.1)	17	-0.046	n.s.	0
b x M-D cervix	17	0.017	n.s.	0
b/B-L cervix	16	0.166	n.s.	3%

Notes: n = number of elements in sample

r = correlation coefficient

sig level = significance level of correlation

r^2 = the proportion of the variance explained by the regression expressed as a percentage.

Table 4.10: Regression values for $\log_{10}$average enamel thickness (c/e, Figure 4.1) on $\log_{10}$variable in Homo

Variable	n	r	sig level	r^2
M-D crown length	12	0.371	n.s.	14%
M-D cervix length	13	0.226	n.s.	5%
M-D x B-L crown	12	0.399	n.s.	16%
M-D x B-L cervix	13	0.207	n.s.	4%
EDJ length (e, Figure 4.1)	13	-0.152	n.s.	2%
Dentine area (b, Figure 4.1)	13	-0.196	n.s.	4%
b x M-D cervix	13	-0.107	n.s.	1%
b/B-L cervix	13	-0.270	n.s.	7%

Table 4.11: Regression values for $\log_{10}$average enamel thickness (c/e, Figure 4.1) on $\log_{10}$variable in Pongo

Variable	n	r	sig level	r^2
M-D crown length	17	-0.172	n.s.	3%
M-D cervix length	17	-0.136	n.s.	2%
M-D x B-L crown	17	-0.048	n.s.	0
M-D x B-L cervix	17	-0.251	n.s.	6%
EDJ length (e, Figure 4.1)	17	-0.072	n.s.	1%
Dentine area (b, Figure 4.1)	17	-0.370	n.s.	14%
b x M-D cervix	17	-0.385	n.s.	15%
b/B-L cervix	17	-0.324	n.s.	10%

Notes: As for Tables 4.8 and 4.9.

(f) Average enamel thickness:

The univariate statistics for average enamel thickness (c/e, Figure 4.1) are shown in Table 4.13. The 95% confidence limits for the population, or species, mean values show that the mean values for average enamel thickness differ between each of the African apes and humans with Pongo's mean value overlapping the lower end of the probable range of the species mean of Homo. Pan has the thinnest enamel, Gorilla has somewhat thicker enamel and Pongo has thicker enamel still, with values overlapping the 95% confidence limits of the human species mean. Thus when reasonable size samples are available the mean values of average enamel thickness distinguish between these taxa even without considering the size of the animals.

The 95% confidence limits for the sample show an overlap between all of the four species although the same ranking may be derived from this data as for the 95% confidence limits for the means. It is necessary that comparisons between species be made with reference to the size of the animal if better separation between the species is to be achieved. Enamel thickness will therefore be compared with dentine area ((b), Figure 4.1) an estimate of body size.

The average enamel thickness results are shown in Figure 4.18 plotted against dentine area ((b), Figure 4.1), univariate statistics of dentine area are given in Table 4.12. There is considerable overlap between Homo and Pongo although Pongo tends to have somewhat thinner enamel than does Homo in spite of being somewhat larger. There is

Table 4.12: Univariate statistics of dentine area (b, Figure 4.1).

	Pan	Gorilla	Homo	Pongo
Sample size	14	18	15	17
Mean (mm^2)	36.96	76.67	33.21	45.75
Minimum	22.3	60.1	18.8	34.5
Maximum	54.9	107.6	45.6	53.7
Range mid-point	38.6	83.85	32.2	44.1
S. Deviation	8.52	12.70	6.82	4.87
Variance	72.54	161.25	46.57	23.76
V_{cor}	23.46	16.79	20.89	10.81
S. Error (S.E.)	2.28	2.99	1.76	1.18
Sample low 95%	18.56	49.87	18.57	35.41
Sample high 95%	55.35	103.46	47.85	56.08
Mean low 95%	32.04	70.35	29.43	43.24
Mean high 95%	41.87	82.98	36.99	48.25
$\frac{(S.E. \times 100)}{Mean}$	6.16	3.90	5.31	2.58

Table 4.13: Univariate statistics of average enamel thickness (c/e, Figure 4.1).

	Pan	Gorilla	Homo	Pongo
Sample size	14	17	13	17
Mean (mm)	0.60	0.87	1.25	1.07
Minimum	0.46	0.62	0.82	0.83
Maximum	0.74	1.14	1.80	1.36
Range mid-point	0.60	0.88	1.31	1.10
S. Deviation	0.100	0.126	0.290	0.141
Variance	0.010	0.016	0.084	0.020
V_{cor}	16.94	14.63	23.68	13.35
S. Error (S.E.)	0.027	0.031	0.081	0.034
Sample low 95%	0.385	0.607	0.618	0.772
Sample high 95%	0.818	1.141	1.884	1.369
Mean low 95%	0.544	0.808	1.075	0.998
Mean high 95%	0.659	0.940	1.426	1.143
$\frac{(S.E. \times 100)}{Mean}$	4.41	3.55	6.44	3.19

Notes: Minimum = the minimum observed value

Maximum = the maximum observed value

V_{cor} = coefficient of variation corrected for small sample size (Pilbeam, 1969 p.10)

Sample low 95% = lower 95% confidence limit

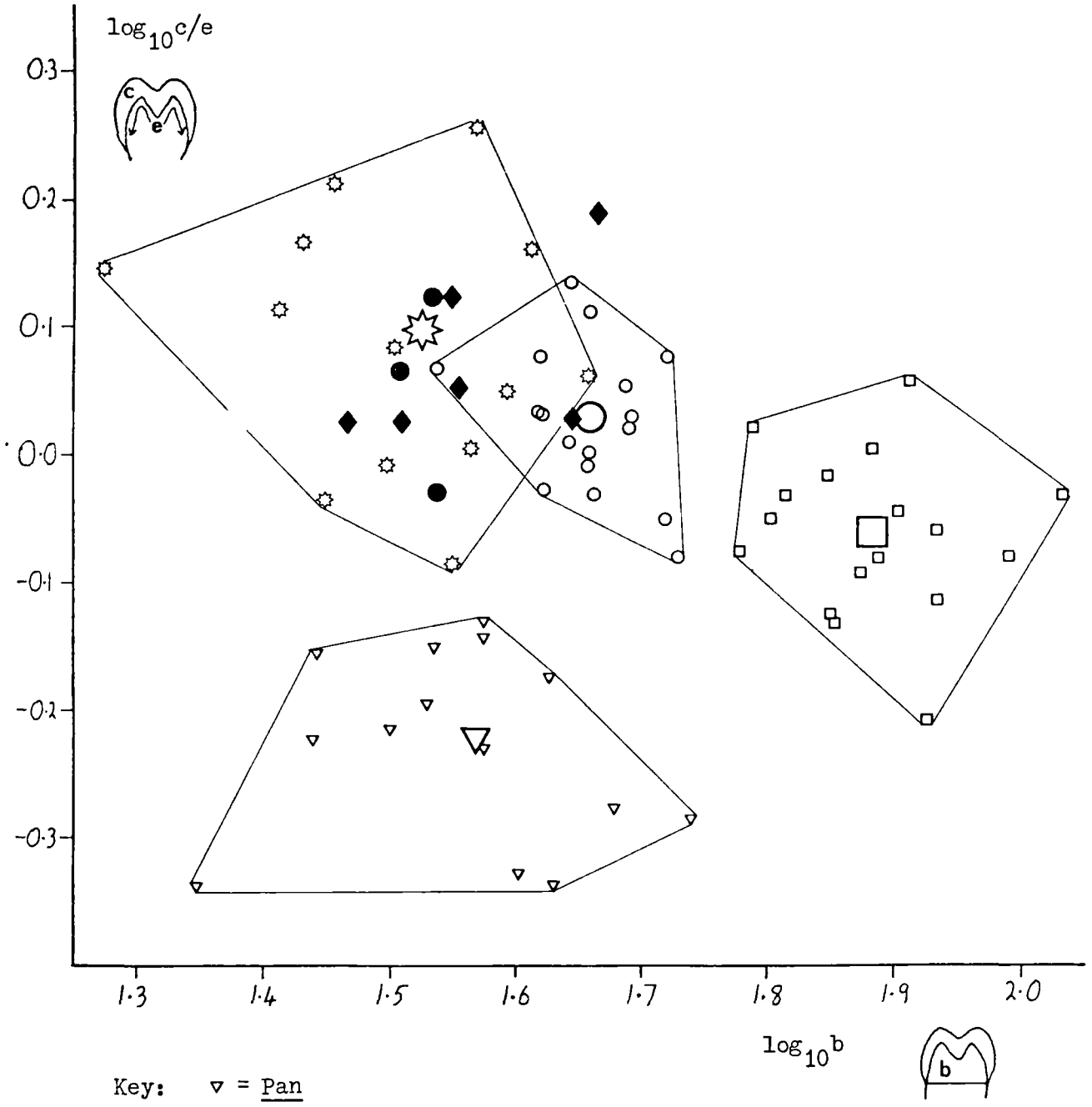
Sample high 95% = upper 95% confidence limit

Mean low 95% = lower 95% confidence limits of the mean

Mean high 95% = upper 95% confidence limits of the mean

$\frac{(S.E. \times 100)}{Mean}$ = Standard error as a percentage of the mean. This can be used as a guide to the adequacy of the sample size (Pilbeam, 1969 p.9)

Figure 4.18: Average enamel thickness (c/e, Figure 4.1) in relation to dentine area (b, Figure 4.1)



Key: ▽ = Pan
□ = Gorilla
☼ = Homo
○ = Pongo
◆ = Pasalar specimen
● = Siwalik specimen

The large symbols are the species mean values.

some overlap between Gorilla and Homo and Pongo although the greater size of Gorilla separates this species on the plot.

The values for the later Miocene hominoid specimens are also shown in Figure 4.18. They invariably fall within the human and orang-utan ranges, although they overlap with the upper end of the observed range of Gorilla average enamel thickness (c/e, Figure 4.1). The size of the teeth tend to place the later Miocene sample into the human range. In other words their enamel is thicker relative to tooth size than is the bulk of the orang-utan sample. The apparent exception, BP 14, is explained by the fact that this tooth is heavily worn (see Figure 4.13j,k) which has reduced the value of average enamel thickness (c/e).

These results agree with those of Gantt (1977) in identifying orang-utan and human enamel as thick. The samples which I have examined suggest that orang-utan enamel is only marginally less thick than human enamel. In addition it is clear that Gorilla has enamel which is quite thick in absolute terms. It is only when the large size of the teeth of this species is taken into account that its enamel can be said to be relatively thin. The results presented here show that Sivapithecus species have thick enamel as has been suggested by other workers on the basis of their pattern of dental wear.

Figure 4.19a shows average enamel thickness (c/e) plotted against dentine volume (b x cervical mesial- distal length). This plot completely separates the four modern taxa and duplicates the relative

enamel thickness results described above. Figure 4.19b shows average enamel thickness (c/e) plotted against average dentine height (b/cenical breadth mesial). The same pattern emerges but with less clear separation between the species along the x-axis (size).

For comparison with Kay's (1981) results, based on his relation of enamel thickness measurements against M-D crown length, results on this are included here. The within species correlation is poor (Table 4.8 - 4.11) but better than the correlation between average enamel thickness and M-D cervix length. This confirms that crown length is by no means an independant variable. These two plots are shown in Figures 4.19c and 4.19d.

Crown area has been suggested to be a better measurement of body size than is crown length (Gingerich, et al, 1982). Results using this measurement of size are shown in Figure 4.19e. Figure 4.19f shows enamel thickness plotted against the cervical length of the tooth multiplied by the cervical breadth across the mesial cusps. The correlation between crown area and enamel thickness (Tables 4.8 - 4.11) in each species is the result of the fact that this measurement of tooth size includes an element of enamel thickness. There is no significant relationship between the cervix area (= tooth size less the contribution of the enamel) and average enamel thickness. It is clear, therefore, that the use of crown dimensions which include enamel in their measurement is unjustifiable on empirical, as well as on a priori, grounds.

No matter which measurement of size is used for between species comparisons of average enamel thickness (c/e) the results are consistent. Homo has the thickest enamel, Pongo has the second thickest enamel relative to tooth size. Gorilla has thicker enamel than does Pan but some of this difference may be explained by tooth (and therefore body) size differences (see below). The specimens of Sivapithecus have thick enamel relative to their tooth size, often in the range of Pongo but overlapping considerably with the position in Homo. In several cases, particularly with the least worn fossil specimens, the later Miocene sample has relatively thicker enamel than Pongo.

Figure 4.19: Log_{10}/log_{10} plots showing average enamel thickness (c/e, Figure 4.1) against dental measurements of size. The dental measurements of size (on the x-axis) are as follows:

Plot A; Dentine area (b, Figure 4.1) x mesial to distal length of the cervix, this approximates dentine volume. (mm^3)

Plot B; Dentine area/the cervical breadth across the mesial cusps, this approximates the average height of the dentine. (mm)

Plot C; Mesial to distal crown length. (mm)

Plot D; Mesial to distal cervix length. (mm)

Plot E; Mesial to distal crown length x buccal to lingual crown breadth. (mm^2)

Plot F; Mesial to distal cervix length x buccal to lingual cervix breadth across the mesial cusps. (mm^2)

The distribution of values is shown as the minimum polygon which contains all of the specimens from one species.

The symbols are as follows: ▽ = Pan mean value

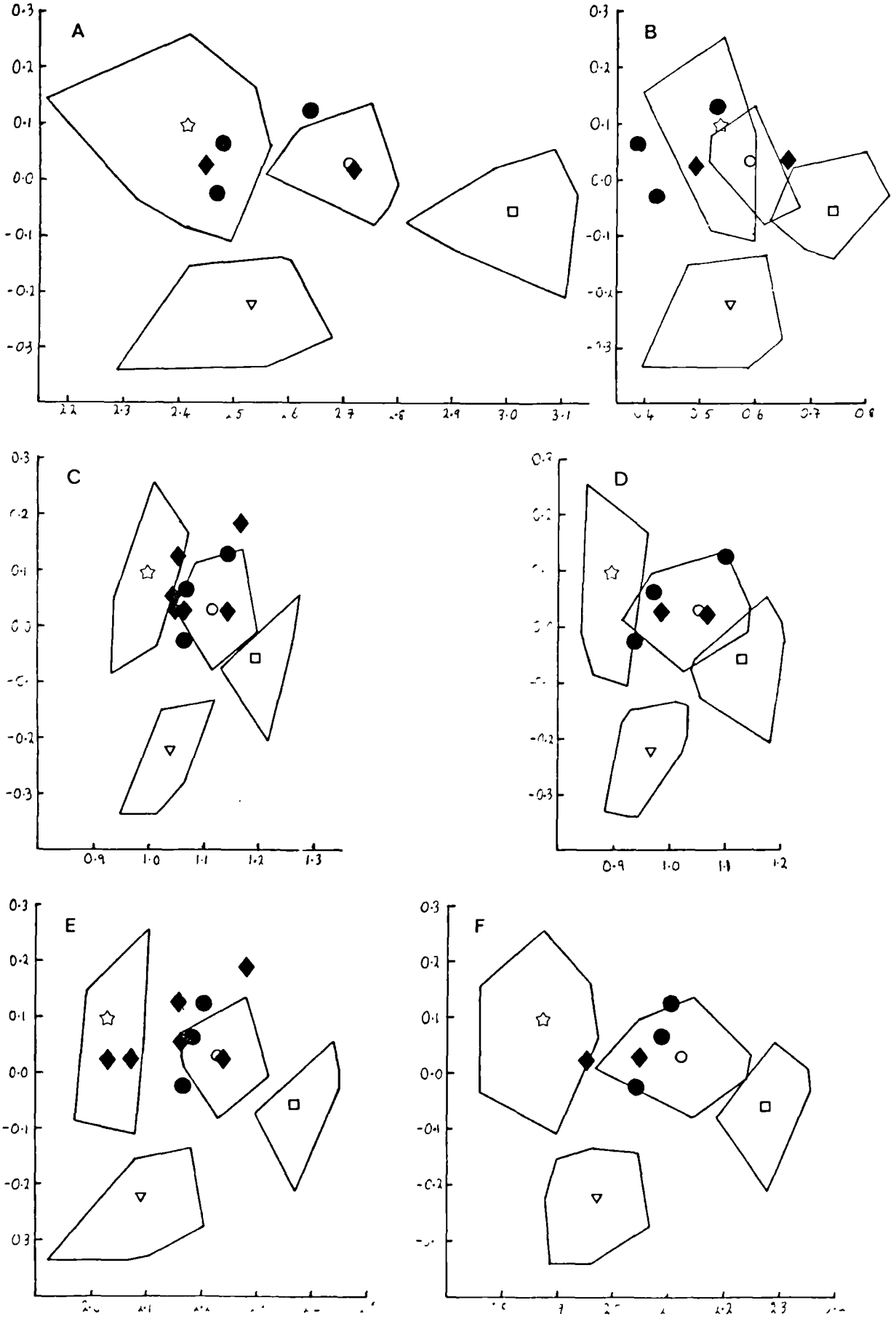
□ = Gorilla mean value

☆ = Homo mean value

○ = Pongo mean value

◆ = Pasalar specimen

● = Siwalik specimen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(g) Linear measurements of enamel thickness

The measurement of average enamel thickness (c/e, Figure 4.1) is not one which has previously been used so it is important to assess whether these results correspond with the linear dimensions used by Gantt (1977) and Kay (1981).

(i) Enamel cap perimeter length divided by enamel dentine junction length (d/e, Figure 4.1).

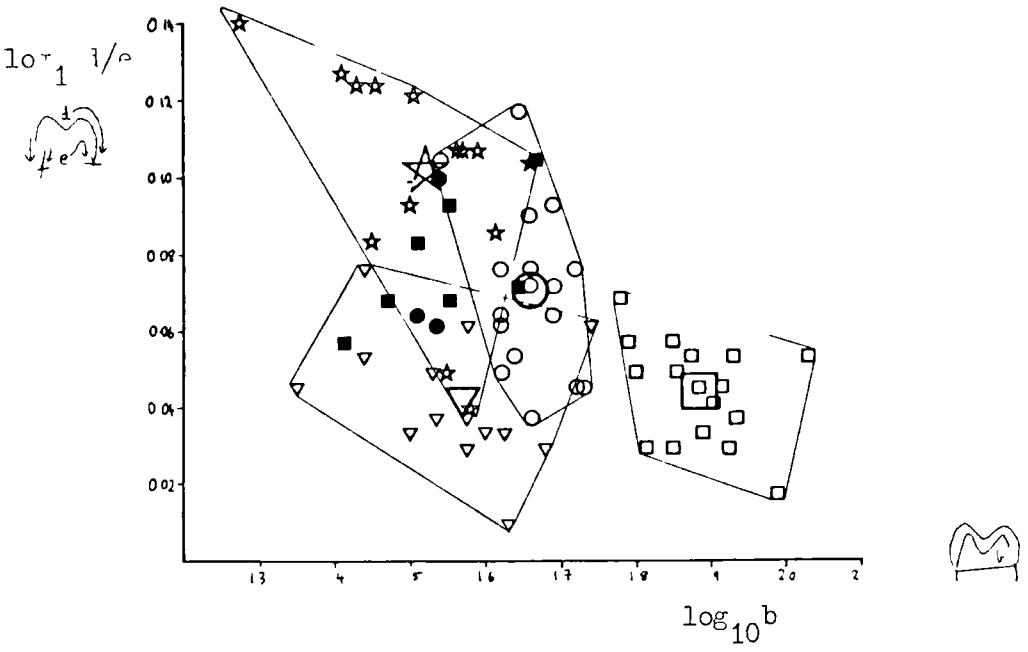
This index produces an indirect measurement of enamel thickness, its relationship with dentine area ((b), Figure 4.1) is shown in Figure 4.20. This index is much less effective in separating the four modern species than is average enamel thickness. If this index is to measure enamel thickness in a consistent way then a constant morphology of the enamel-dentine junction is assumed. In other words a constant relationship between the perimeter length of the enamel cap and the length of the enamel-dentine junction must be assumed. This rather complicated measurement, effectively comparing the radii of two shapes, provides the same pattern of relative enamel thickness results as does average enamel thickness but the degree of overlap between Homo, Pongo and Pan would make the results from this index less useful.

Table 4.14: Univariate statistics of enamel cap perimeter length divided by enamel-dentine (d/e, Figure 4.1) for the sample in Figure 4.20.

	Pan	Gorilla	Homo	Pongo
Sample size	14	17	14	17
Mean	1.10	1.11	1.26	1.18
Minimum	1.02	1.04	1.10	1.09
Maximum	1.19	1.17	1.38	1.31
Range mid-point	1.11	1.11	1.24	1.20
S. Deviation	0.043	0.033	0.061	0.060
Variance	0.0018	0.011	0.[illegible]5	0.0036
V_{cor}	3.977	3.052	6.55	5.146
S. Error (S.E.)	.012	0.008	0.022	0.015
Sample low 95%	1.009	1.037	1.190	1.050
Sample high 95%	1.195	1.088	1.439	1.304
Mean low 95%	1.091	1.099	1.243	1.163
Mean high 95%	1.114	1.115	1.286	1.192
$\frac{(S.E. \times 100)}{Mean}$	1.04	0.73	1.71	1.23

Notes: As for Tables 4.12 and 4.13.

Figure 4.20: Enamel cap perimet r length/enamel-dentine junction l ngth (d/e, Figure 4.1), as a measure of enamel thickness, in relation to dentine area. Th's index of enamel thickness is dimensionless and the y-axis has been adjusted to match those for linear measurements of enamel hickness (Figs. 4.21 - 4.24).



y: ▽ = Pan

□ = Gorilla

☆ = Homo

○ = Pongo

■ = Pasalar specimen

● Siwalik specimen

The lar e symbols are the species mean values.

(ii) Cuspal enamel thickness:

One of the measurements used by Gantt (1977) was the vertical thickness of the enamel over the cusp tips (my measurements (f) and (g), Figure 4.2). I have shown that these measurements are extremely susceptible to variations in the position of the saw cut (see serial sections; III, 2). Table 4.15 gives the univariate statistics of measurement (f) (vertical thickness of the enamel over the buccal cusp tip), and Figure 4.21a shows this variable plotted against dentine area. This measurement of enamel thickness is more variable than the measurement of average enamel thickness except in the case of Pongo. The thick enamelled Miocene hominoids tend to have an equal or greater thickness of enamel than does Pongo for this variable for slightly smaller teeth.

The vertical thickness of enamel over the lingual cusp (g) is shown in Figure 4.21b and the univariate statistics of this variable in Table 4.16. The measurement is more variable than the same measurement on the buccal cusps, but duplicates the results.

Table 4.15: Univariate statistics of the vertical thickness of the enamel over the buccal cusp tip (f, Figure 4.2) for the samples in Figure 4.21a.

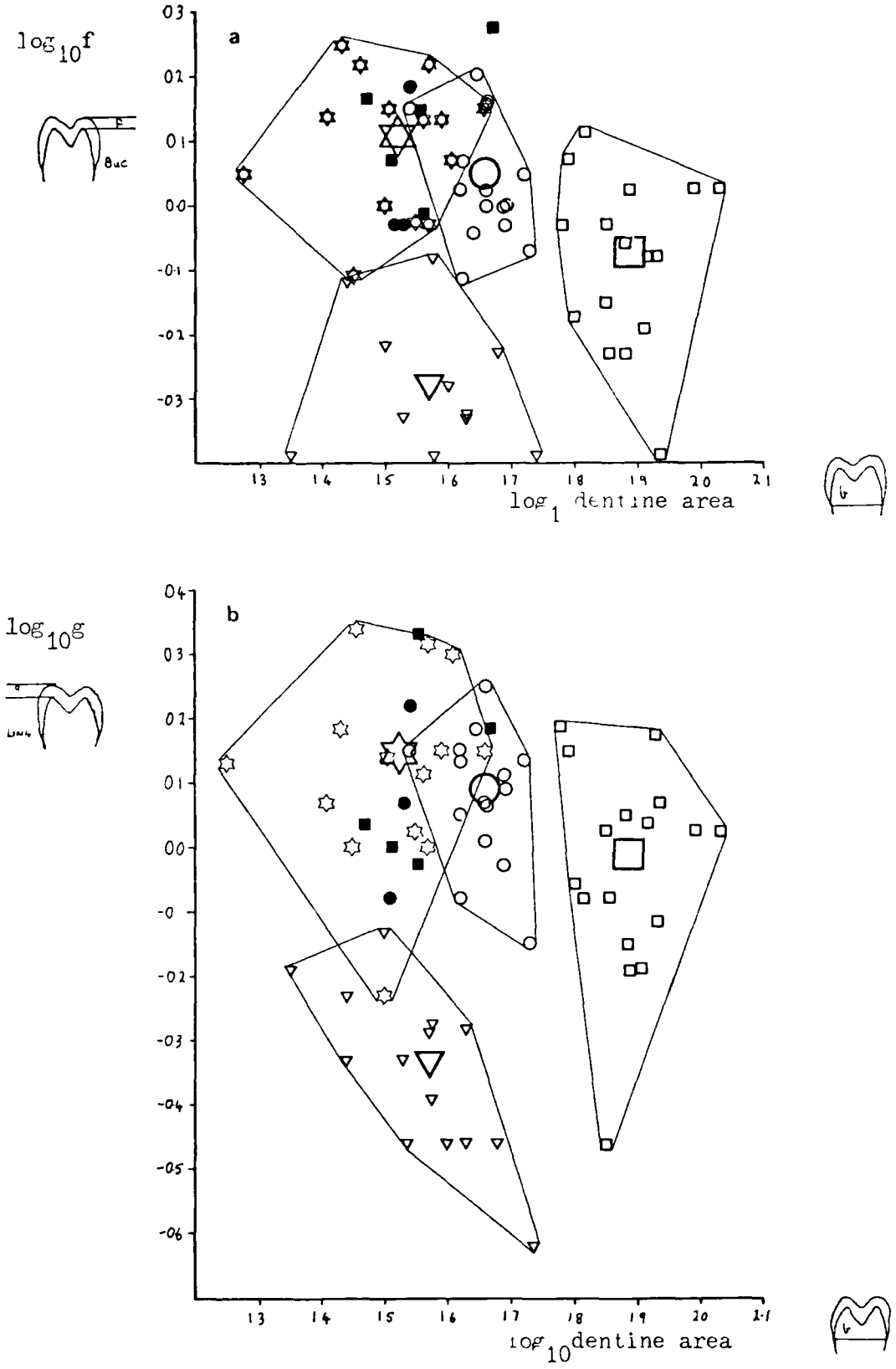
	Pan	Gorilla	Homo	Pongo
Sample size	12	16	14	16
Mean (mm)	0.53	0.86	1.28	1.12
Minimum	0.35	0.41	0.77	0.77
Maximum	0.83	1.30	1.77	1.59
Range mid-point	0.59	0.86	1.27	1.18
S. Deviation	0.15	0.24	0.30	0.23
Variance	0.022	0.059	0.092	0.054
V_{cor}	28.86	28.76	24.03	20.22
S. Error (S.E.)	0.04	0.06	0.08	0.06
Sample low 95%	0.20	0.34	0.63	0.67
Sample high 95%	0.85	1.37	1.94	1.67
Mean low 95%	0.43	0.73	1.11	1.00
Mean high 95%	0.62	0.99	1.46	1.23
$\frac{(S.E. \times 100)}{Mean}$	8.16	7.08	6.31	5.21

Table 4.16: Univariate statistics of the vertical thickness of the enamel over the lingual cusp tip (g, Figure 4.2) for the samples in Figure 4.21b.

	Pan	Gorilla	Homo	Pongo
Sample size	15	18	14	16
Mean (mm)	0.46	0.98	1.39	1.22
Minimum	0.24	0.35	0.59	0.71
Maximum	0.74	1.53	2.18	1.77
Range mid-point	0.49	0.94	1.39	1.24
S. Deviation	0.13	0.31	0.44	0.27
Variance	0.018	0.099	0.198	0.071
V_{cor}	29.47	32.65	32.53	22.19
S. Error (S.E.)	0.04	0.07	0.12	0.07
Sample low 95%	0.17	0.31	0.43	0.65
Sample high 95%	0.75	1.64	2.35	1.79
Mean low 95%	0.39	0.82	1.14	1.08
Mean high 95%	0.54	1.13	1.65	1.36
$\frac{(S.E. \times 100)}{Mean}$	7.48	7.59	8.54	5.46

Not · As for Tables 4.12 and 4.13.

Figure 4.21: Cuspal enamel thickness in relation to dentine area (b, Figure 4.1).



Key: As for Figure 4.20.

(iii) Occlusal basin enamel thickness:

The measurements of the thickness of the enamel in the occlusal basin (h, i, j, see Figure 4.2) are shown plotted against dentine area in Figure 4.22. The univariate statistics of these measurements are shown in Tables 4.17 - 4.19. Measurements (h) and (i) are less variable than the measurements of enamel thickness over the cusp tips. This is probably because these measurements are less prone to errors resulting from minor differences in the plane of measurement (Figure 4.6 and 4.7). Measurement (j), the thickness in the centre of the occlusal basin is much more variable. This is probably the result of the fact that it is difficult to define the position of the top of the enamel as in many teeth the enamel is deeply grooved at this position. The results from measurement (j) are therefore difficult to interpret but the other occlusal measurements repeat the pattern of relative enamel thickness with Homo having the thickest enamel, Pongo second thickest and Pan and Gorilla the thinnest.

Table 4.17: Univariate statistics of the radial thickness of the enamel on the occlusal (lingual) aspect of the buccal cusp (h, Figure 4.2) for the samples in Figure 4.22a.

	Pan	Gorilla	Homo	Pongo
Sample size	16	17	14	18
Mean (mm)	0.63	0.91	1.22	1.21
Minimum	0.40	0.64	0.92	0.86
Maximum	0.81	1.30	1.89	1.53
Range mid-point	0.61	0.97	1.41	1.20
S. Deviation	0.11	0.19	0.29	0.19
Variance	0.012	0.036	0.086	0.037
V_{cor}	17.66	21.34	24.52	16.22
S. Error (S.E.)	0.027	0.046	0.078	0.046
Sample low 95%	0.39	0.50	0.58	0.80
Sample high 95%	0.86	1.31	1.85	1.61
Mean low 95%	0.57	0.81	1.05	1.11
Mean high 95%	0.68	1.00	1.39	1.30
$\frac{(S.E. \times 100)}{Mean}$	4.34	5.10	6.44	3.77

Table 4.18: Univariate statistics of the radial thickness of the enamel on the occlusal (buccal) aspect of the lingual cusp (i, Figure 4.2) for the samples in Figure 4.22b.

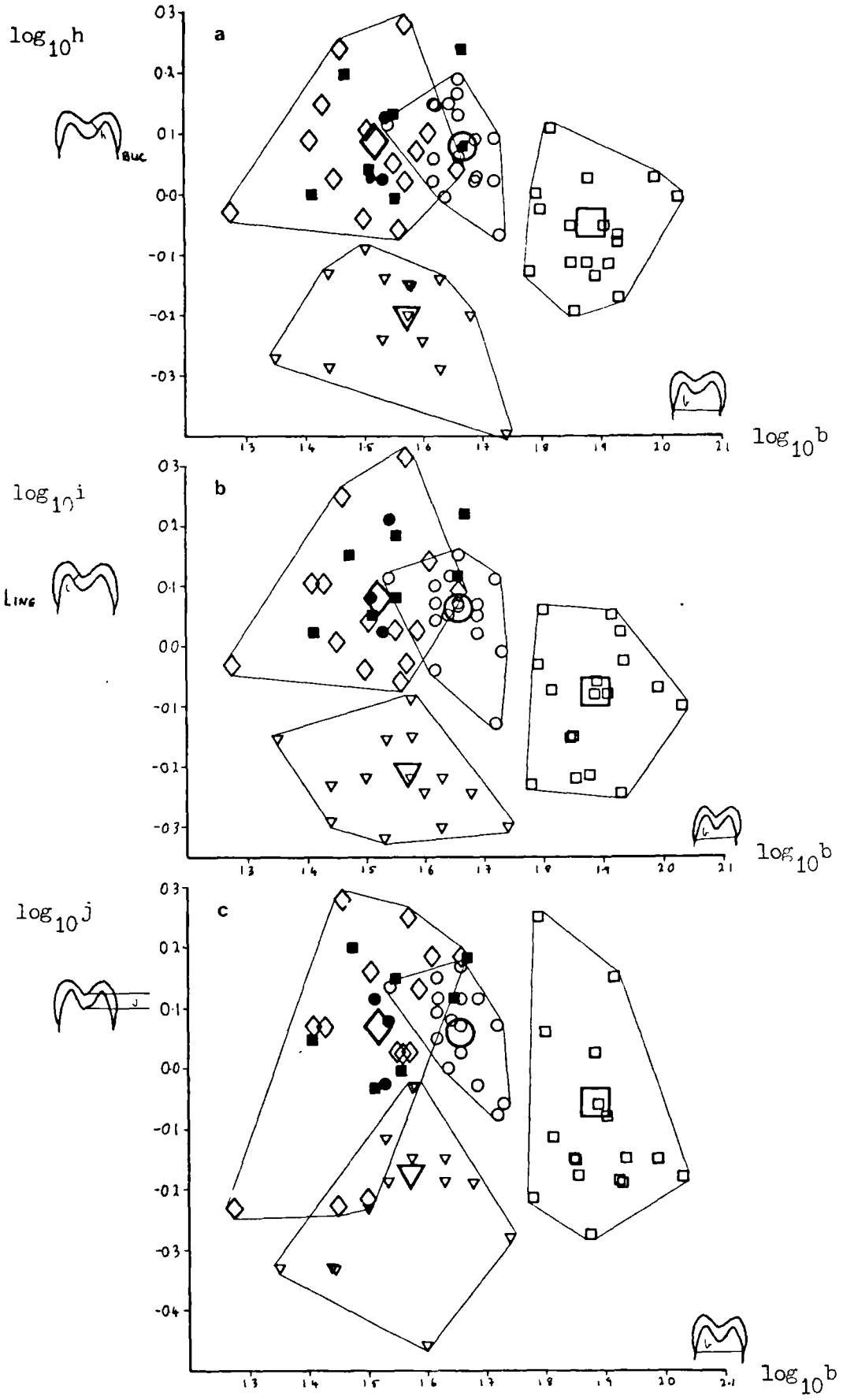
	Pan	Gorilla	Homo	Pongo
Sample size	16	17	14	18
Mean (mm)	0.61	0.85	1.21	1.16
Minimum	0.48	0.57	0.87	0.74
Maximum	0.81	1.19	2.06	1.42
Range mid-point	0.65	0.86	1.47	1.08
S. Deviation	0.10	0.21	0.35	0.17
Variance	0.009	0.043	0.119	0.028
V_{cor}	16.17	24.72	29.12	14.72
S. Error (S.E.)	0.02	0.05	0.09	0.04
Sample low 95%	0.40	0.41	0.46	0.80
Sample high 95%	0.81	1.29	1.95	1.51
Mean low 95%	0.55	0.75	1.01	1.07
Mean high 95%	0.66	0.96	1.41	1.24
$\frac{(S.E. \times 100)}{Mean}$	3.98	5.91	7.65	3.42

Table 4.19: Univariate statistics of the vertical thickness of the enamel in the centre of the occlusal fovea (j, Figure 4.2) for the samples in Figure 4.22c.

	Pan	Gorilla	Homo	Pongo
Sample size	16	17	15	17
Mean (mm)	0.67	0.88	1.17	1.15
Minimum	0.35	0.53	0.59	0.83
Maximum	1.06	1.77	1.91	1.47
Range mid-point	0.71	1.15	1.25	1.15
S. Deviation	0.19	0.34	0.43	0.20
Variance	0.038	0.117	0.183	0.041
V_{cor}	29.48	39.31	37.21	17.76
S. Error (S.E.)	0.05	0.08	0.11	0.05
Sample low 95%	0.25	0.16	0.25	0.73
Sample high 95%	1.08	1.61	2.09	1.58
Mean low 95%	0.58	0.71	0.93	1.05
Mean high 95%	0.77	1.06	1.41	1.26
$\frac{(S.E. \times 100)}{Mean}$	7.26	9.39	9.45	4.25

Notes: As for Tables 4.12 and 4.13.

Figure 4.22: Occlusal basin enamel thickness in relation to dentine area (b, Figure 4.1).



Key: As for Figures 4.20 and 4.21, but Homo = ◇

(iv) Lateral crown enamel thickness:

The measurements of enamel thickness on the lateral aspects of the crown (k-n) are shown in Figures 4.23 and 4.24. The univariate statistics of these variables are given in Tables 4.20 - 4.23. These measurements are less variable than measurements (f), (g) and (j), probably because they are not subject to great variability resulting from the plane of the saw cut as they are below the level where the conical cusps tend to produce oblique sections with minor shifts in the position of the saw cut. Interestingly there is less distinction between Homo, Pongo, Sivapithecus and the African apes than was the case for the occlusal enamel thickness. This suggests that the thick enamel in Homo, Pongo and Sivapithecus is thickest, in comparison with the African apes, on the occlusal surface. Alternatively it may be the case that the enamel is thinnest on the occlusal portions in the African apes or that the lateral enamel is relatively thin in Homo, Pongo and Sivapithecus. Nonetheless all of these measurements show the same set of relationships of relative enamel thickness as the occlusal measurements although the distinction between the species is less clear. This may raise a further problem with regard to the measurement employed by Kay (1981) (see discussion below).

Table 4.20: Univariate statistics of the radial thickness of the enamel on the lateral aspect of the buccal cusp (k, Figure 4.2) for the samples in Figure 4.23a.

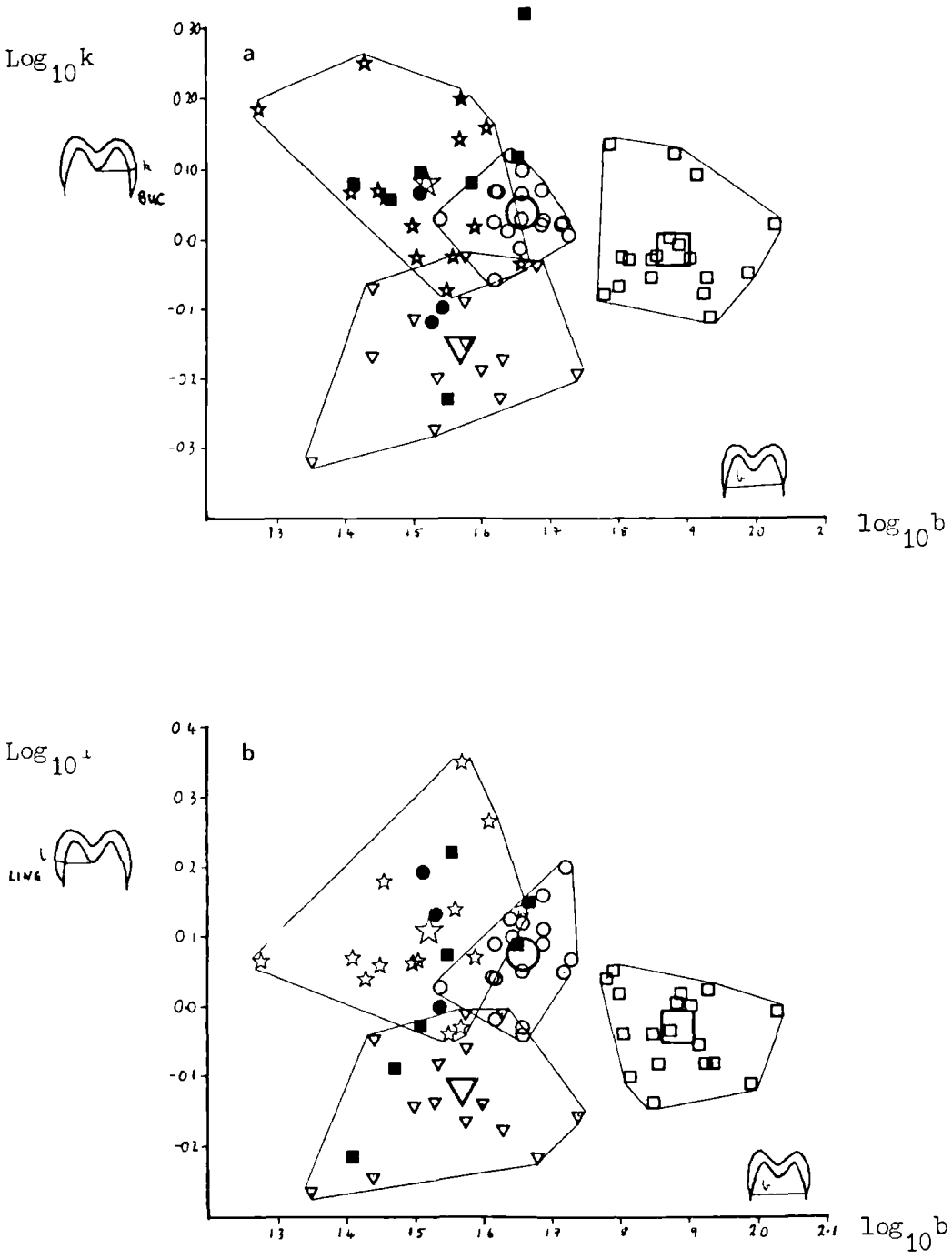
	Pan	Gorilla	Homo	Pongo
Sample size	16	18	15	18
Mean (mm)	0.70	0.98	1.20	1.10
Minimum	0.48	0.77	0.84	0.87
Maximum	0.94	1.36	1.79	1.32
Range mid-point	0.71	1.07	1.32	1.10
S. Deviation	0.14	0.17	0.28	0.11
Variance	0.021	0.028	0.079	0.013
V_{cor}	21.01	17.36	23.73	10.40
S. Error (S.E.)	0.04	0.04	0.07	0.03
Sample low 95%	0.39	0.62	0.60	0.86
Sample high 95%	1.01	1.33	1.80	1.34
Mean low 95%	0.62	0.89	1.05	1.04
Mean high 95%	0.78	1.06	1.36	1.16
$\frac{(S.E. \times 100)}{Mean}$	5.18	4.04	6.03	2.42

Table 4.21: Univariate statistics of the radial thickness of the enamel on the lateral aspect of the lingual cusp (l, Figure 4.2) for the samples in Figure 4.23b.

	Pan	Gorilla	Homo	Pongo
Sample size	16	18	15	18
Mean (mm)	0.77	0.93	1.28	1.19
Minimum	0.54	0.73	0.91	0.92
Maximum	1.11	1.12	2.24	1.57
Range mid-point	0.83	0.93	1.58	1.25
S. Deviation	0.16	0.12	0.36	0.17
Variance	0.027	0.014	0.129	0.030
V_{cor}	21.59	12.80	28.52	14.66
S. Error (S.E.)	0.04	0.03	0.09	0.04
Sample low 95%	0.42	0.68	0.51	0.83
Sample high 95%	1.11	1.18	2.05	1.56
Mean low 95%	0.68	0.87	1. 8	1.11
Mean high 95%	0.85	0.99	1.48	1.28
$\frac{(S.E. \times 100)}{Mean}$	5.31	2.98	7.25	3.41

Notes: As for Tables 4.12 and 4.13.

Figure 4.23: Radial thickness of the enamel on the lateral aspects of the tooth in relation to dentine area (b, Figure 4.1).



Key: As for Figures 4.20 and 4.21.

Table 4.22: Univariate statistics of the horizontal thickness of the enamel on the lateral aspect of the buccal cusp (m, Figure 4.2) for the samples in Figure 4.24a.

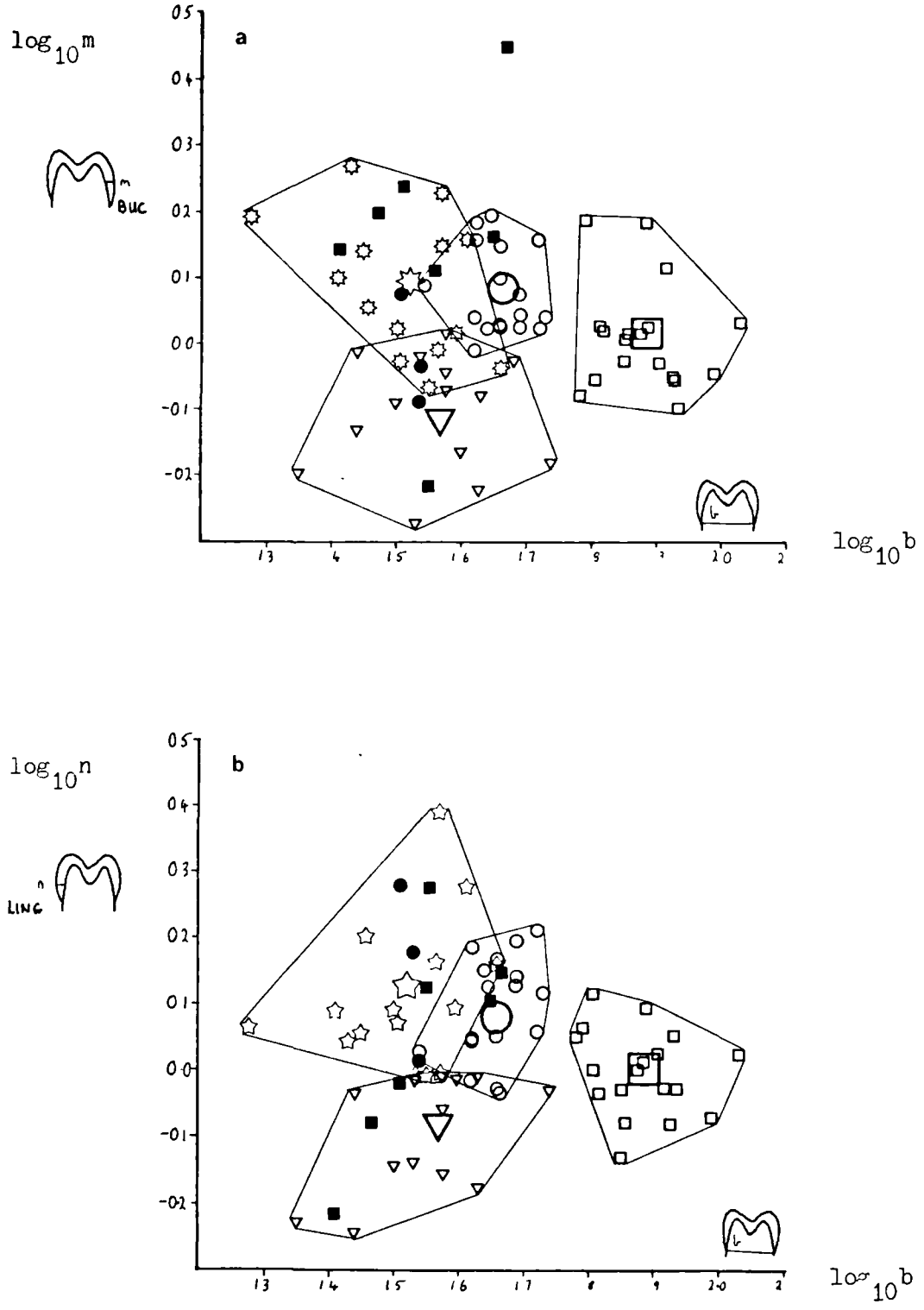
	Pan	Gorilla	Homo	Pongo
Sample size	16	18	15	18
Mean (mm)	0.76	1.04	1.24	1.22
Minimum	0.50	0.80	0.86	0.98
Maximum	1.03	1.53	1.86	1.57
Range mid-point	0.77	1.17	1.36	1.28
S. Deviation	0.16	0.21	0.31	0.18
Variance	0.027	0.045	0.093	0.034
V_{cor}	21.68	20.72	24.95	15.35
S. Error (S.E.)	0.04	0.05	0.08	0.04
Sample low 95%	0.42	0.59	0.59	0.83
Sample high 95%	1.11	1.49	1.90	1.61
Mean low 95%	0.68	0.94	1.08	1.13
Mean high 95%	0.85	1.15	1.41	1.31
$\frac{(S.E. \times 100)}{Mean}$	5.33	4.82	6.34	3.57

Table 4.23: Univariate statistics of the horizontal thickness of the enamel on the lateral aspect of the lingual cusp (n, Figure 4.2) for the samples in Figure 4.24b.

	Pan	Gorilla	Homo	Pongo
Sample size	15	18	15	18
Mean (mm)	0.83	1.00	1.34	1.21
Minimum	0.57	0.74	0.97	0.92
Maximum	1.23	1.30	2.44	1.63
Range mid-point	0.90	1.02	1.71	1.28
S. Deviation	0.18	0.15	0.39	0.27
Variance	0.03	0.02	0.16	0.07
V_{cor}	22.48	14.99	30.07	22.61
S. Error (S.E.)	0.05	0.04	0.10	0.06
Sample low 95%	0.44	0.69	0.49	0.64
Sample high 95%	1.23	1.32	2.18	1.78
Mean low 95%	0.73	0.93	1.12	1.07
Mean high 95%	0.94	1.08	1.55	1.34
$\frac{(S.E. \times 100)}{Mean}$	5.71	3.48	7.64	5.26

Notes: As for Tables 4.12 and 4.13.

Figure 4.24: Horizontal thickness of the enamel on the lateral aspects of the tooth ir relation to dentine area (b, Figure 4.1).



Key: As for Figure 4.20.

(v) Enamel-dentine junction morphology:

Simons (1976) suggested that "thick-enamelled" species (Homo, Ramapithecus but not Pongo) had relatively flat dentine surfaces. The actual height of the conical portion of the dentine was therefore measured for the buccal cusp (o) and the lingual cusp (p). The univariate statistics for these variables are given in Tables 4.24 and 4.25 respectively. The values are shown in Figures 4.25a and b plotted against dentine area. The results are similar for both cusps. What emerges is that Pongo has relatively low dentine horns in comparison to the area of the dentine (b) (Tables 4.24 and 4.25). This is not the case for Homo which appears to be little different to the relative value for Pan and Gorilla. This is completely the reverse of Simons (1976) prediction and makes it more difficult to explain why Pongo teeth exhibit a "thin enamelled" wear pattern (Simons 1976) (see discussion below). The sample of Sivapithecus overlaps with the range of values found in Homo, Pan and Pongo but tend be towards the low end of the range for Pan and Homo which suggests that these forms have a enamel-dentine junction morphology most similar to that in Pongo.

Table 4.24: Univariate statistics of the vertical height of the dentine horn of the buccal cusp (o, Figure 4.2) for the samples in Figure 4.25a.

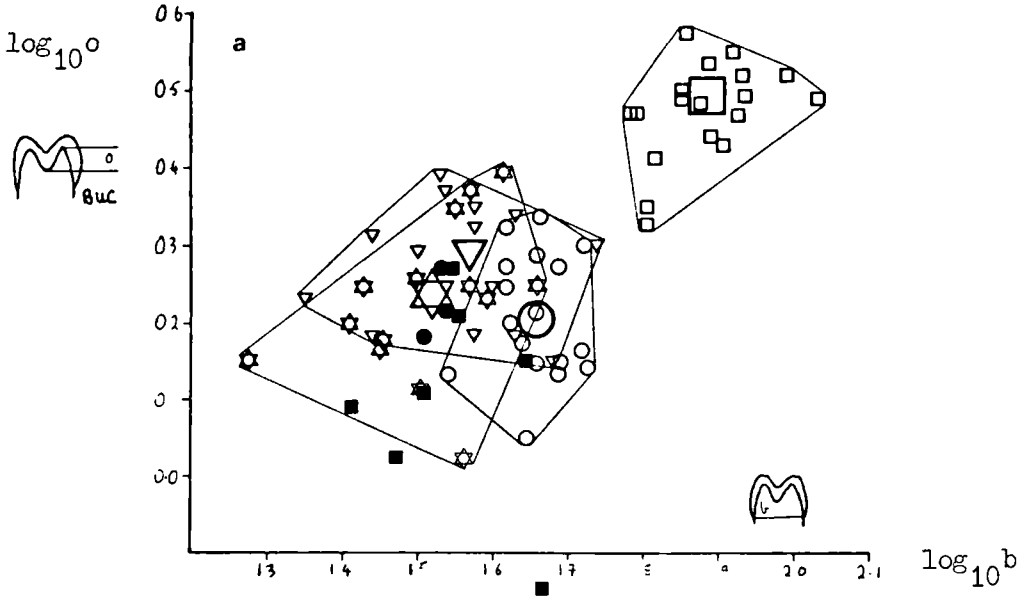
	Pan	Gorilla	H mo	Pongo
Sample size	16	18	14	18
Mean (mm)	1.96	3.01	1.73	1.62
Minimum	1.42	2.12	1.06	1.00
Maximum	2.48	3.77	2.48	2.18
Range mid-point	1.95	2.95	1.77	1.59
S. Deviation	0.35	0.42	0.40	0.34
Variance	0.121	0.173	0.162	0.114
V_{cor}	17.99	14.00	23.59	21.16
S. Error (S.E.)	0.09	0.10	0.11	0.08
Sample low 95%	1.22	2.13	0.87	0.90
Sample high 95%	2.70	3.89	2.60	2.33
Mean low 95%	1.78	2.80	1.50	1.45
Mean high 95%	2.15	3.22	1.97	1.78
$\frac{(S.E. \times 100)}{Mean}$	4.43	3.26	6.19	4.92

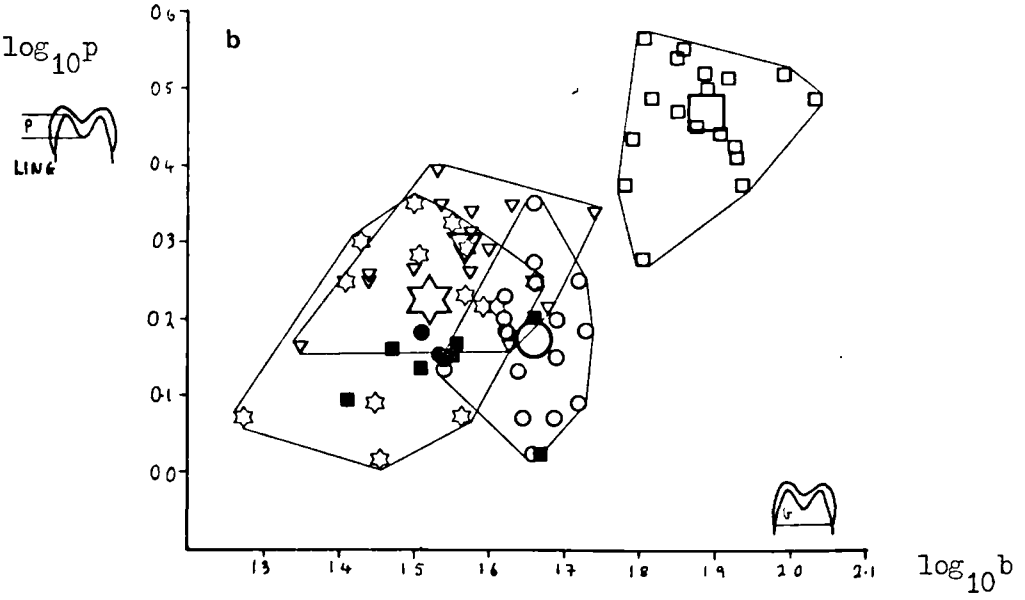
Table 4.25: Univariate statistics of the vertical height of the dentine horn of the lingual cusp (p, Figure 4.2) for the samples in Figure 4.25b.

	Pan	Gorilla	Homo	Pongo
Sample size	16	18	14	18
Mean (mm)	1.98	2.95	1.67	1.49
Minimum	1.47	1.91	1.04	0.94
Maximum	2.48	3.66	2.24	2.24
Range mid-point	1.98	2.79	1.64	1.59
S. Deviation	0.31	0.46	0.38	0.32
Variance	0.095	0.216	0.144	0.102
V_{cor}	15.84	16.00	23.06	21.67
S. Error (S.E.)	0.08	0.11	0.10	0.08
Sample low 95%	1.32	1.96	0.85	0.82
Sample high 95%	2.64	3.93	2.49	2.17
Mean low 95%	1.81	2.71	1.45	1.34
Mean high 95%	2.14	3.18	1.89	1.65
$\frac{(S.E. \times 100)}{Mean}$	3.90	3.72	6.05	5.04

Notes: As for Tables 4.12 and 4.13.

Figure 4.25: Vertical height of the dentine horns in relation to dentine area (b, Figure 4.1).





Key: As for Figure 4.20.

5. Relative enamel thickness taking account of size

It is necessary to include some aspect of size when comparing enamel thickness between species of differing body size. The most useful way to do this would be a single number which summarises enamel thickness for the species and allows for the size of the animal. The limited data available suggest that enamel thickness scales at a slope of about 0.33 on body weight for Anthropoidea (Gantt, 1977; Kay, 1981). An index of relative enamel thickness must compare two variables which scale equivalently (i.e. have the same slope) in order to be size independant. There are insufficient data to calculate regressions for tooth size measurements, which exclude the contribution of the enamel, on body weight. However, it is reasonable to assume, until empirical data are available, that different measurements of the size of the tooth will scale equivalently with body size since they are all so closely interconnected being part of a single structure (the tooth).

Dentine area has been selected as a useful dental estimate of body size which does not include any enamel dimensions in its magnitude (Figure 4.17). It seems likely that an area measurement of tooth size will scale with a higher slope than will the linear measurements of enamel thickness. The average enamel thickness (c/e, Figure 4.1) is the best single summary of enamel thickness for a tooth. Table 4.26 gives results for a relative enamel thickness index calculated by expressing average enamel thickness (c/e, Figure 4.1) as a percentage of the square root of dentine area (b, Figure 4.1). This means that the index is dimensionless and that the probable differences in slope of an area and a linear dimension have been removed. This may leave

some scaling differences relating to the values of the intercepts but these will be relatively insignificant (Hills, personal communication). Some univariate statistics for this relative enamel thickness index are included in Table 4.26. Finally the mean values for a number of other possible indices are given all of which show an identical pattern of relative enamel thickness. These are:

1) Enamel cap area expressed as a percentage of dentine area (c/b, Figure 4.1) which is similarly dimensionally balanced but whose interpretation is complicated by the fact that the numerator is not a direct enamel thickness measurement.

2) Average enamel thickness expressed as a percentage of enamel-dentine junction length ((c/e)/e, Figure 4.1). This index is also dimensionless but suffers from the disadvantage that the size variable (enamel-dentine junction length, (e), Figure 4.1) is involved in the calculation of average enamel thickness.

3) Finally average enamel thickness is expressed as a percentage of the cube root of body weight. If body weight can be assumed to be equivalent to a volume measurement then this index is also dimensionless. This index has the disadvantage that it can only be used for species whose body weight is known and cannot therefore be applied to fossil species without recourse to entirely circular arguments. It should be noted that the value for Homo for this index (Table 4.26) makes the (invalid) assumption of modern body weight for the archaeological human sample for which enamel thickness data were calculated.

The important point is that each of these four possible indices of

relative enamel thickness produce the same pattern of results. This tends to confirm the validity of the results from them. For reasons explained above the preferred index is the one which expresses average enamel thickness (c/e, Figure 4.1) as a percentage of the square root of dentine area (b, Figure 4.1). This has the advantage that it is not only dimensionally balanced and probably size independant, an assumption which will be evaluated empirically when the data are available for a wider range of primates, but also that it is simple to interpret. The numerator is average enamel thickness which is the most concise summary of the distribution of the enamel over the tooth crown, the denominator is a dental estimate of body size which does not include any enamel component in its magnitude. In some ways it seems more reasonable to assume that average enamel thickness (c/e, Figure 4.1) and the square root of dentine area (b, Figure 4.1) will show equal allometry, being parts of the same functional complex (i.e. the tooth), than to assume that average enamel thickness will scale isometrically with the cube root of body weight, a relationship which has not been demonstrated empirically, since body weight involves many more factors than do different dental measurements taken on the same tooth. Relative enamel thickness is therefore defined as the index expressing average enamel thickness as a percentage of the square root of dentine area:

$$\text{Relative enamel thickness} = \frac{c/e \times 100.}{\sqrt{b}} \quad \text{(See Figure 4.1)}$$

The results for the relative enamel thickness index (Table 4.26) separate the extant hominoids into three groups with no overlap of the

Table 4.26: Relative enamel thickness in extant and extinct Hominoidea

Index		Pan	Gorilla	Homo	Pongo	Hylobates	Siw	Pas	Siva
$\frac{c/e}{\sqrt{b}}$ x 100	Sample size	14	17	13	17	1	3	6	9
	Mean	10.10	10.04	22.35	15.93	11.02	19.73	19.71	19.71
	Minimum	7.02	6.75	13.76	11.32	-	16.10	16.07	16.07
	Maximum	13.31	13.39	32.26	20.45	-	22.66	22.68	22.68
	Range mid-point	10.17	1 .07	23.01	15.89	-	19.38	19.38	19.38
	S. Deviation	2.09	1.74	6.23	2.51	-	3.33	2.49	2.58
	Variance	4.35	3.01	38.83	6.27	-	11.12	6.22	6.67
	V_{cor}	21.01	17.53	28.42	15.96	-	18.31	13.18	13.46
	S. Error (S.E.)	0.56	0.42	1.73	0.61	-	1.93	1.02	0.86
	Sample low 95%	5.60	6.38	8.77	10.62	-	5.38	13.30	13.76
	Sample high 95%	14.60	13.70	35.93	21.24	-	34.08	26.12	25.66
	Mean low 95%	8.90	9.15	18.58	14.65	-	11.45	17.09	17.73
	Mean high 95%	11.30	10.93	26.12	17.21	-	28.01	22.33	21.69
	$\frac{(S.E. \times 100)}{Mean}$	5.52	4.19	7.73	3.81	-	9.76	5.17	4.37
c/b x 100	Mean	32	31	67	46	-	59	57	57
$\frac{c/e}{e}$ x 100	Mean	3.21	3.26	7.46	5.45	-	6.65	6.85	6.78
$\frac{c/e}{\sqrt[3]{B.W.}}$ x 100	Mean	1.68	1.80	3.00	2.84	-	-	-	-

Notes: Siw = Siwalik hominoid sample (see Appendix A)

Pas = Pasalar hominoid sample (see Appendix A)

Siva = Combined Siwalik and Pasalar sample (Sivapithecus)

$\frac{c/e}{\sqrt{b}}$ x 100 = Average enamel thickness expressed as a percentage of the square root of dentine area

c/b x 100 = Enamel cap area expressed as a percentage of dentine area

$\frac{c/e}{e}$ x 100 = Average enamel thickness expressed as a percentage of enamel-dentine junction length

$\frac{c/e}{\sqrt[3]{B.W.}}$ x 100 = Average enamel thickness expressed as a percentage of the cube root of body weight.

Univariate statistics defined as for Tables 4.12 and 4.13.

95% confidence limits for the mean value of the index. The first group with the thinnest enamel comprises Pan and Gorilla, the single specimen of Hylobates falls into this category. The second category of intermediate thickness of enamel contains Pongo. The thickest enamel is found in Homo. The later Miocene hominoid sample of Sivapithecus overlaps the lower end of the Homo 95% confidence limits for the mean and falls above the 95% confidence limits for the mean for Pongo. The observed range of relative enamel thickness separate the group with thin enamel (Pan, Gorilla and probably Hylobates) from the genera with thicker enamel but the observed range for relative enamel thickness overlaps between the intermediate thickness category (Pongo) and the thick category (Home and Sivapithecus). The 95% confidence limits for the mean value for relative enamel thickness clearly show that Sivapithecus has thicker enamel than does Pongo overlapping the lower end of the 95% confidence limits for the mean of relative enamel thickness for Homo. However, this is not evidence that Sivapithecus has thinner enamel than Homo. It should also be borne in mind that Homo is probably microdont, this may be the result of its having relatively small dentine and pulp components as there is no evidence that the enamel thickness in Homo has reduced. The clear resolution of this question requires a sample of Australopithecus and/or Paranthropus teeth to be sectioned for enamel thickness (and enamel microstructure, see Chapter 5) determination. If the dentine portion of the teeth of Homo is responsible for the relatively small teeth in this genus this would explain why the 95% confidence limits for the mean value of relative enamel thickness extend beyond the upper 95% confidence limit for the mean value of

relative enamel thickness in Sivapithecus, which also has thick enamel.

If the assumption that Homo is microdont is accepted then it is more likely to be the result of a reduction in the dentine portion of the tooth than the enamel. The enamel thickness is determined by the period during which the enamel is formed and the daily formation rate. There is certainly no evidence that human teeth form for a shorter period than those of later Miocene hominoids, if anything the reverse seems more likely given the long maturation period in humans. A slower daily formation rate of enamel in Homo seems unlikely (this is determined in Chapter 5). Thus it appears likely that the relatively small teeth in Homo result from a smaller dentine and pulp portion which would have the effect of slightly increasing the relative enamel thickness index.

Thus three groups of relative enamel thickness are recognised. Firstly a group with thin enamel (Pan, Gorilla and probably Hylobates), secondly a group with intermediate thickness of enamel (Pongo) and finally a group with thick enamel (Homo and Sivapithecus). The observed range for the relative enamel thickness index (Table 4.26) show that the intermediate thickness category is more similar to the thick category than to the thin enamel category. In terms of the commonly used terms "thick-enamelled" and "thin-enamelled" the former term would apply to Homo, Sivapithecus and Pongo, the latter category to Pan, Gorilla and Hylobates. These terms however obscure the clear distinction between Pongo and the thicker

enamelled Sivapithecus and Homo. It would be preferable to talk in terms of the numerical values of the relative enamel thickness index but descriptive names can be applied. Species with thin enamel are those with mean values of relative enamel thickness between 8.90 and 11.30, species with intermediate/thick enamel are those with mean values of relative enamel thickness between 14.65 and 17.25, species with thick enamel are those with mean values of relative enamel thickness between 17.70 and 26.20. The category to which Pongo belongs is termed intermediate/thick because there is clearly room for an intermediate/thin category with mean values for relative enamel thickness between 11.30 and 14.65.

Using these metrically defined categories which take the animals size into account Pan, Gorilla and Hylobates have thin enamel, there are no taxa with intermediate/thin enamel currently documented, Pongo has intermediate/thick enamel and Homo and Sivapithecus have thick enamel. The thinner enamel in Pongo compared to Sivapithecus and Homo probably explains why its dentine exposure pattern is different to that in Sivapithecus, Australopithecus, Paranthropus and (often) Homo and superficially similar to the dentine exposure pattern in the African apes and in Hylobatidae.

IV. COMPARISON OF RESULTS WITH PREVIOUS STUDIES

1. Introduction

The best summary of absolute enamel thickness is the enamel cap area (c, Figure 4.1) divided by the length of the enamel-dentine junction (e, Figure 4.1) which produces an average enamel thickness dimension for the plane of section (c/e). I have shown that this dimension provides data which allow useful comparisons to be made between the species sampled, and it is less variable than most of the linear dimensions. Unfortunately this dimension has not been used in previous metrical studies of enamel thickness (Gantt, 1977; Kay 1981) although Gantt had the sections available to do this. Gantt (1977) found that measurements of cuspal enamel thickness, my measurements f and g (Figure 4.2), were most useful in separating species. However, results for these dimensions have been shown to be excessively variable as a result of slight differences in the position of the saw cut (Figures 4.6, 4.7 and 4.8, Tables 4.5, 4.15 and 4.16). The problem therefore is whether any of the linear measurements can be used to summarise enamel thickness for a species. If this is possible then it will allow the combination of my results with those achieved by Gantt (1977) and Kay (1981) for a wider range of primates.

2. Comparison of average enamel thickness (c/e, Figure 4.1) with single linear measurements

In order to determine whether any of the linear measurements of enamel thickness employed by Gantt (1977) and Kay (1981) could be

combined with my average enamel thickness results, regressions were calculated for each variable on average enamel thickness (c/e, Figure 4.1) to determine how closely single linear measurements of enamel thickness correlated with average enamel thickness. The results of these regressions for each variable are given in Tables 4.27 - 4.35. Each species is first considered separately, and these regressions show how well any linear dimension estimates average enamel thickness for that species. In addition, three sets of combined data are shown with species grouped together forming monophyletic groups. In almost all cases the correlations are poor for two or more of the individual species. Correlations for data for species combined into monophyletic groups, and particularly for the great ape and human clade, are always significant but the exactness of the correlation is not as good as one would wish. The higher correlations for the combined species as compared to single species probably results from the calculation of the correlation across a wider range of values. The higher correlation coefficient does not mean that linear measurements predict average enamel thickness (c/e, Figure 4.1) precisely. The standard deviation of the regression (S.yx, Tables 4.27 - 4.35) may be used to quantify how exactly the linear dimension predicts average enamel thickness. For the combined species regressions the standard deviation of the regressions are at least as great, or greater, than the standard deviations of the regressions for single species. This means that the use of a single linear measurement to predict average enamel thickness (c/e, Figure 4.1) is not made more precise by using a wide range of species despite the higher correlation coefficient.

Table 4.27: Regression of (f) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	11	0.493	0.152	0.659	0.108	0.145	0.126
Gorilla	16	0.319	0.239	0.694	0.112	0.242	0.229
Homo	13	0.731	0.371	0.750	0.291	0.298	0.203
Pongo	15	0.712	-0.189	1.206	0.142	0.241	0.169
Pan + Gorilla	27	0.660	0.017	0.925	0.184	0.258	0.194
Pan + Gorilla + Homo	40	0.847	-0.032	1.025	0.317	0.384	0.204
Pan + Gorilla + Homo + Pongo	55	0.841	-0.046	1.052	0.288	0.360	0.195

Table 4.28: Regression of (g) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.246	0.266	0.337	0.100	0.137	0.133
Gorilla	17	0.269	0.381	0.690	0.126	0.324	0.312
Homo	13	0.837	-0.192	1.291	0.291	0.448	0.245
Pongo	15	0.889	-0.665	1.740	0.141	0.276	0.126
Pan + Gorilla	31	0.667	-0.268	1.357	0.179	0.363	0.270
Pan + Gorilla + Homo	44	0.850	-0.249	1.334	0.315	0.494	0.260
Pan + Gorilla + Homo + Pongo	59	0.862	-0.275	1.368	0.292	0.463	0.235

Table 4.29: Regression of (h) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.488	0.293	0.559	0.100	0.115	0.100
Gorilla	17	0.724	-0.048	1.091	0.126	0.190	0.131
Homo	13	0.806	0.188	0.834	0.291	0.301	0.178
Pongo	17	0.511	0.463	0.705	0.141	0.194	0.167
Pan + Gorilla	31	0.822	0.051	0.971	0.179	0.211	0.120
Pan + Gorilla + Homo	44	0.899	0.104	0.901	0.315	0.315	0.138
Pan + Gorilla + Homo + Pongo	61	0.863	0.098	0.951	0.287	0.316	0.160

Table 4.30: Regression of (i) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.413	0.364	0.397	0.100	0.096	0.087
Gorilla	17	0.517	0.110	0.851	0.126	0.208	0.178
Homo	13	0.827	-0.019	0.997	0.291	0.350	0.197
Pongo	17	0.586	0.386	0.720	0.141	0.173	0.140
Pan + Gorilla	31	0.713	0.117	0.830	0.179	0.208	0.146
Pan + Gorilla + Homo	44	0.879	0.033	0.948	0.315	0.339	0.162
Pan + Gorilla + Homo + Pongo	61	0.865	0.033	0.980	0.287	0.325	0.163

Notes: n = sample size used in regression calculation
r = correlation coefficient
y/x = intercept
S.x = standard deviation of average enamel thickness (c/e) for the sample used in the regression
S.y = standard deviation of the linear enamel thickness measurement for the sample used in the regression
S.yx = standard deviation of the regression, calculated from the formula
$S.yx \triangleq \sqrt{(1-r^2)}(S.y)$

Table 4.31: Regression of (j) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.616	-0.008	1.070	0.100	0.174	0.137
Gorilla	17	0.711	-0.799	1.925	0.126	0.342	0.240
Homo	13	0.624	0.043	0.936	0.291	0.436	0.341
Pongo	16	0.345	0.692	0.450	0.145	0.190	0.178
Pan + Gorilla	31	0.710	-0.130	1.201	0.179	0.302	0.213
Pan + Gorilla + Homo	44	0.766	0.031	0.969	0.315	0.398	0.256
Pan + Gorilla + Homo + Pongo	60	0.757	0.050	0.979	0.289	0.373	0.244

Table 4.32: Regression of (k) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.330	0.433	0.451	0.100	0.137	0.129
Gorilla	17	0.753	0.082	1.025	0.126	0.172	0.113
Homo	13	0.641	0.409	0.617	0.291	0.280	0.215
Pongo	17	0.426	0.739	0.329	0.141	0.109	0.099
Pan + Gorilla	31	0.804	0.153	0.935	0.179	0.208	0.124
Pan + Gorilla + Homo	44	0.815	0.315	0.708	0.315	0.273	0.158
Pan + Gorilla + Homo + Pongo	61	0.805	0.336	0.691	0.287	0.246	0.146

Table 4.33: Regression of (l) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.765	0.100	1.082	0.100	0.142	0.091
Gorilla	17	0.406	0.593	0.390	0.126	0.121	0.111
Homo	13	0.715	0.235	0.879	0.291	0.357	0.250
Pongo	17	0.462	0.570	0.575	0.141	0.175	0.155
Pan + Gorilla	31	0.735	0.361	0.653	0.179	0.159	0.108
Pan + Gorilla + Homo	44	0.858	0.208	0.875	0.315	0.321	0.165
Pan + Gorilla + Homo + Pongo	61	0.838	0.221	0.873	0.287	0.299	0.163

Table 4.34: Regression of (m) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.232	0.557	0.358	0.100	0.154	0.150
Gorilla	17	0.698	-0.020	1.212	0.126	0.219	0.157
Homo	13	0.561	0.501	0.576	0.291	0.298	0.247
Pongo	17	0.048	1.145	0.065	0.141	0.190	0.190
Pan + Gorilla	31	0.734	0.199	0.959	0.179	0.233	0.158
Pan + Gorilla + Homo	44	0.744	0.399	0.678	0.315	0.287	0.192
Pan + Gorilla + Homo + Pongo	61	0.698	0.425	0.677	0.287	0.278	0.199

Table 4.35: Regression of (n) on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	13	0.451	0.398	0.688	0.102	0.156	0.139
Gorilla	17	0.368	0.615	0.446	0.126	0.153	0.142
Homo	13	0.690	0.213	0.941	0.291	0.396	0.287
Pongo	17	0.439	0.504	0.708	0.141	0.227	0.204
Pan + Gorilla	30	0.624	0.444	0.632	0.177	0.179	0.140
Pan + Gorilla + Homo	43	0.813	0.268	0.878	0.313	0.338	0.197
Pan + Gorilla + Homo + Pongo	60	0.786	0.272	0.890	0.284	0.322	0.199

Notes: As for Tables 4.27 - 4.30.

It seems possible that part of the problem might result from having data for upper and lower molars combined, particularly for measurements f, g, k, l, m, and n (Figure 4.2) (Gantt, 1977), so regressions were calculated for these variables for upper and lower molars separately. The correlations were sometimes improved but often had lower correlation coefficients. Therefore the problem appears to be that the linear measurements are not related in a highly correlated fashion with average enamel thickness (c/e, Figure 4.1). The reasons why this should be the case are not entirely clear. Most of the linear measurements are more variable than average enamel thickness within a sample (see S.x and S.y columns in Tables 4.27 - 4.35). Two causes might be responsible for this, firstly, obliquity of section has more influence on the linear measurements than it does on average enamel thickness (Figures 4.6 and 4.7), secondly local variations in enamel thickness at different sites on the tooth may have considerable influence on a single linear dimension, but will have much less influence on average enamel thickness (c/e, Figure 4.1).

A further complication in using a linear measurement of enamel thickness to summarise the distribution of the enamel over the tooth is that the regression equation between the linear value and average enamel thickness varies from one species to another. This means that if a linear dimension of enamel thickness is used to approximate average enamel thickness then the regression equation for the species concerned must be known. In other words the same value of a linear enamel thickness dimension will result in different estimates of

average enamel thickness for different species. The use of any linear dimension to approximate average enamel thickness assumes that the regression equation between the linear dimension and average enamel thickness is constant for the species being examined. This is not the case even within the great ape and human clade. This implies that not only is the average thickness of enamel different between the species of great apes and man, but that the enamel is differently distributed over the tooth in each species. This is an area which requires further study but it is confirmation that the use of simple linear measurements of enamel thickness is undesirable.

3. Comparison of average enamel thickness (c/e, Figure 4.1) with averaged linear measurements.

One problem which was encountered in recording the linear measurements involved the orientation of the section. Minor changes in the allignment of the plane across the two cusp tips produced large differences in the magnitudes of the measurements of low lateral enamel thickness (k, l, m and n, Figure 4.2) depending whether the measurement was taken above or below the cingular bulge. Examples where this problem may be distorting the data may be seen in Figures 4.12 h, 4.14 c, i, j, 4.15 b, d, g. One way to correct for these possible errors is to average the measurements from the buccal and the lingual cusps. This will also remove possible differences between the thickness of the enamel on one side of upper and lower teeth which Gantt (1977) reported.

Regression values for averaged data from buccal and lingual enamel thicknesses are given in Tables 4.36 and 4.37. In almost every case this combination of data results in better correlation with average enamel thickness for individual species, and in every case it provides a more significant correlation when data from more than one species is combined. The slope and intercept values for the combined sample of Pan, Gorilla, Homo and Pongo suggest that, in general, thin enamelled species will have relatively thick low lateral enamel, and/or thick enamelled species will have relatively thin low lateral enamel. This implies that for species with high values of average enamel thickness the enamel is concentrated towards the occlusal surface and is less

thickened on the lateral aspects of the tooth.

The three measurements (h, i and j) summarising occlusal enamel thickness have also been combined for each specimen and their regression values with average enamel thickness (c/e) are given in Table 4.38. The correlations were significant for measurements (h) and (i) (Tables 4.29 and 4.30) probably because these are not subject to the same problems of obliquity as the cusp tip measurements. The averaging of the three measurements of occlusal enamel thickness produces a highly correlated relationship when the four species are combined. For the combined species sample the relationship is nearly isometric and the intercepts are close to zero. This suggests that the average enamel thickness is highly correlated with occlusal enamel thickness and that the relationship between the two dimensions of enamel thickness is isometric. In other words, thicker enamelled species do NOT have relatively thicker occlusal enamel than the thin enamelled species. This implies that the less than isometric relationship between average enamel thickness and low lateral enamel thickness means that thin enamelled species have relatively thick lateral enamel and that thick enamelled species have relatively thin lateral enamel. It seems likely that this is because different selective factors act on lateral enamel thickness than on occlusal enamel thickness. When a tooth is worn so that most or all of the occlusal enamel has been destroyed the exposed dentine is less resistant to wear. The band of lateral enamel is the only thing which prevents the tooth from breaking up and allows the tooth to wear away gradually, and this prolongs the tooth's life especially taking into

account the formation of secondary dentine. The value of this effect is comparable to a more familiar situation. If one tries to drive a wooden stake into the ground using a metal hammer the wood tends to split and fall away in chunks. If the wood is fitted with a metal band around the top this prevents it from splitting and greatly increases its ability to resist compressive force. The fact that thin enamelled species have relatively thick lateral enamel suggests that it is functioning in this way and also that there is a minimum thickness which produces this effect. Thick enamelled hominoid species have more lateral enamel than thin enamelled species but there is less increase in this region than there is in occlusal enamel thickness. This suggests that thick enamel serves two purposes: firstly in lateral enamel to resist increased compressive forces, and secondly on the occlusal surface for a different function (see Chapter 6). The less than isometric relationship between lateral enamel thickness and average enamel thickness implies that the thick enamel in thick enamelled species is not solely for resistance to increased compressive forces.

Table 4.36: Regression of $\frac{((k) + (l))}{2}$ on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.725	0.259	0.783	0.100	0.108	0.074
Gorilla	17	0.762	0.334	0.718	0.126	0.119	0.077
Homo	13	0.854	0.325	0.748	0.291	0.255	0.133
Pongo	17	0.582	0.657	0.451	0.141	0.109	0.089
Pan + Gorilla	31	0.886	0.252	0.806	0.179	0.162	0.075
Pan + Gorilla + Homo	44	0.935	0.264	0.792	0.315	0.267	0.095
Pan + Gorilla + Homo + Pongo	61	0.919	0.282	0.782	0.287	0.244	0.096

Table 4.37: Regression of $\frac{((m) + (n))}{2}$ on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	13	0.537	0.440	0.576	0.102	0.109	0.092
Gorilla	17	0.744	0.291	0.840	0.126	0.143	0.096
Homo	13	0.826	0.363	0.755	0.291	0.266	0.150
Pongo	17	0.506	0.779	0.429	0.141	0.119	0.103
Pan + Gorilla	30	0.841	0.296	0.827	0.177	0.174	0.094
Pan + Gorilla + Homo	43	0.909	0.328	0.784	0.313	0.270	0.113
Pan + Gorilla + Homo + Pongo	60	0.888	0.343	0.790	0.284	0.253	0.116

Table 4.38: Regression of $\frac{((h) + (i) + (j))}{2}$ on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	14	0.677	0.220	0.670	0.100	0.099	0.073
Gorilla	17	0.760	-0.244	1.287	0.126	0.214	0.139
Homo	13	0.784	0.072	0.922	0.291	0.342	0.212
Pongo	16	0.577	0.514	0.628	0.145	0.158	0.129
Pan + Gorilla	31	0.835	0.013	1.000	0.179	0.214	0.118
Pan + Gorilla + Homo	44	0.893	0.056	0.940	0.315	0.331	0.149
Pan + Gorilla + Homo + Pongo	60	0.875	0.060	0.970	0.289	0.320	0.155

Notes: As for Tables 4.27 - 4.30.

4. Comparison of average thickness (c/e, Figure 4.1) with all linear measurements combined

Finally, the average enamel thickness (c/e) has been compared with all the linear measurements combined. Table 4.39 gives regression values for the averaged linear measurements (f - n, Figure 4.2) against c/e, and the correlations are much better for all of the samples than was the case for any of the individual measurements. The values of the standard deviation of the regression (S.yx, Table 4.39) show that a large portion of the variation in the y variable is explained by the regression equation. The data given in Tables 4.13 - 4.23 show that the values of average enamel thickness are less variable than most of the linear measurements, as well as being intuitively the best summary of the distribution of enamel over the tooth in the plane of section.

Table 4.39: Regression of $\left(\frac{f + g + h + i + j + k + l + m + n}{9}\right)$ on (c/e).

Taxon	n	r	y/x	slope	S.x	S.y	S.yx
Pan	10	0.853	0.235	0.709	0.112	0.093	0.049
Gorilla	17	0.854	0.107	0.947	0.126	0.140	0.073
Homo	13	0.924	0.194	0.870	0.291	0.273	0.104
Pongo	16	0.860	0.392	0.728	0.137	0.116	0.059
Pan + *Gorilla*	27	0.932	0.104	0.943	0.180	0.182	0.066
Pan + *Gorilla* + *Homo*	40	0.964	0.124	0.921	0.315	0.301	0.080
Pan + *Gorilla* + *Homo* + *Pongo*	56	0.957	0.130	0.932	0.284	0.276	0.080

Notes: As for Tables 4.27 - 4.30.

5. Comparison of results with previous studies

Linear dimensions such as those used by Gantt (1977) and estimated by Kay (1981) are poor approximations of average enamel thickness (c/e). If there is an overriding reason to use a linear dimension, for example to examine occlusal enamel thickness alone, then a number of measurements should be averaged (e.g. Tables 4.36 - 4.38). If a non destructive approach using wear exposed enamel thickness measurements (e.g. Kay, 1981) is to be attempted then either measurements from two or more locations (such as m and n, Figure 4.2) should be averaged (which would required heavily worn teeth to be used) or the severe limitations of the results must now be acknowledged. The fact that lateral enamel thickness is relatively less in thick enamelled species (i.e. its contribution to average enamel thickness is relatively small) produces further limitations on the results from Kay's (1981) method.

Kay (1981) mentions that there are no published data with which to assess the reliability of his estimates. I have therefore sectioned the lower second molars in my sample through the hypoconid and entoconid tips in order to simulate his plane of measurement so as to provide some directly taken measurements for comparison. The measurements resulting are given in Table 4.40, and these show that Kay's (1981) estimates of enamel thickness are considerably greater than the average enamel thickness dimension (c/e). This in itself presents no problem providing that the extent to which the estimate exceeds the average enamel thickness dimension is constant. However,

this does not appear to be the case (Table 4.40). In fact it appears that Kay's (1981) estimate exaggerates enamel thickness in Pongo to a greater extent that in Pan and Gorilla. Kay's estimate of enamel thickness equates most closely with the measurement of the radial thickness of the enamel from the buccal dentine horn tip to the buccal edge of the enamel (s, Figure 4.26). It also equates fairly well with the horizontal thickness of the enamel measured from the buccal dentine horn tip to the buccal edge of the enamel (q, Figure 4.26). These results confirm that Kay (1981) was successful in selecting teeth which were all worn so as to expose homologous regions for enamel thickness measurement. The results are not able to determine whether the measurement which Kay (1981) made is a radial or a horizontal one, although there is an indication that the measurement is not completely horizontal. It seems likely that the section through the enamel produced by wear will be oblique from an observation of worn teeth and Kay (1981) certainly believes that his measurement is a horizontal thickness (Kay, 1981, Figure 1.b).

Three problems exist with the use of the enamel exposure in wear facets as an estimate of enamel thickness (Kay, 1981). Firstly, it assumes that wear facets develop at a constant angle in all primate specie · Grine's (1981) results do not support this assumption. Secondly, the plane of the enamel thickness measurement is oblique, lying below the positions of my measurements q and s (Figure 4.26) but above the level of measurement m (Figures 4.2 and 4.26). The range of levels over which Kay's (1981) measurements may be taken will vary according to the height of the dentine horns in the species sampled.

This appears to show grade differences, as well as size related differences (Figure 4.25). Thirdly, the method assumes that the angle at the tip of the dentine horn is constant in all of the primates which Kay (1981) studied. This assumption is implicit in the use of recognisably oblique sections through the enamel thickness (Kay, 1981, Figure 1.b), and the degree of obliquity, assuming a constant plane of wear across the species sampled, is dependant on the angle subtended by the dentine horns. Figure 4.27 shows two hypothetical cusp sections which have exactly equal radial enamel thickness 5.0 mm. The section in Figure 4.27.a has an apical angle of 100°, and 4.27.b has an apical angle of 60°. Any oblique measurement of the enamel thickness will be greater in the flatter cusp for a constant wear plane. For example, measurement q (Figure 4.26) would be 8.0 mm in the flatter cusp (160% of radial thickness) and 5.2 mm (104% of radial thickness) in the more pointed cusp.

The assumption of a constant dentine horn apical angle implicit in Kay's (1981) method has a further necessary implication. As molar breadth can be shown to be significantly correlated with body size it follows that Kay's method also assumes that the height of the dentine horns in different species can equally be explained by body size differences. The reason why this must be the assumption is shown diagramatically in Figure 4.28. The width of the base of the triangle of the dentine horns is approximately half of the crown width. If the angle of the dentine horns is constant in all higher primate species then teeth of the same width must have the same height of dentine horns by basic trigonometry. Figure 4.28 shows two dentine horns (or

cusps) of equal basal width, they have different height cusps resulting in different apical angles of the dentine horns. My results show that dentine horn height is not entirely explained by size, even within the great ape and human clade (Figure 4.25 and Tables 4.24 and 4.25). Pongo has relatively flat dentine horns which means that Kay's (1981) method would tend to exaggerate enamel thickness to a greater extent in this genus than in the African apes. This is what I found to be the case (Table 4.41, E_m/ average enamel thickness column). The assumptions made by this method of estimating enamel thickness contradict the generally accepted view that some primates have high pointed cusps while others have flatter occlusal surfaces (e.g comparisons of colobinae and cercopithecinae). Simon (1976) firmly believed that dentine horn height, and the morphology of the enamel-dentine junction was a character of adaptive and taxonomic value, not one which could simply be explained by body size differences. Qualitative differences in the apical angle of the dentine horns are readily observable within the anthropoid primates. This means that Kay's (1981) survey of enamel thickness will inevitably overestimate radial enamel thickness in species with relatively flat crowns, to a far greater degree than it will estimate radial enamel thickness in species with high pointed cusps (Figure 4.27). Within the great ape and human clade studied here this will lead to exaggerated enamel thicknesses in Pongo and in the later Miocene Sivapithecus which have relatively flat dentine horns and therefore rather obtuse apical angles of the dentine horns.

These problems with regard to the assumptions implicit in methods

Figure 4.26: Position and orientation of enamel thickness measurements taken on buccal to lingual sections through the hypoconid and entoconid in lower second molars (M_2).

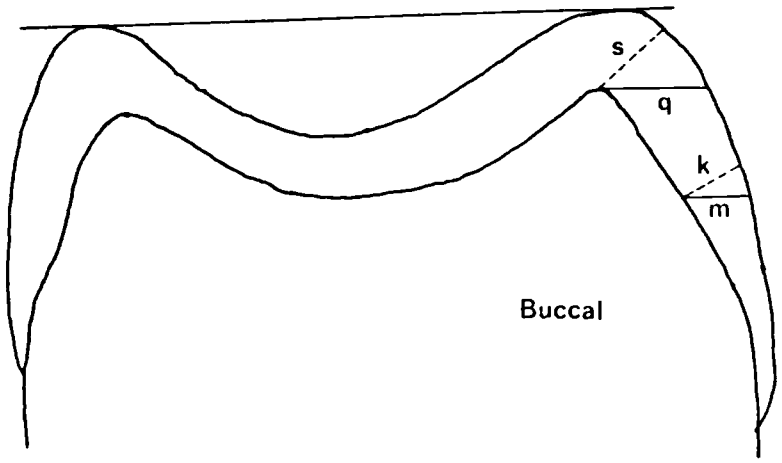


Figure 4.27: The effect of the apical angle of the dentine horns on the enamel thickness as measured by Kay (1981).

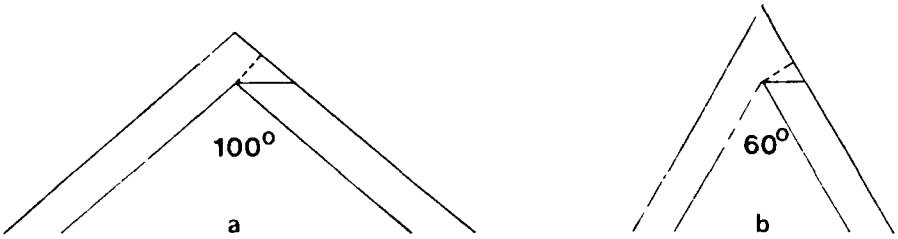


Figure 4.28: The effect of dentine horn apical angle on cusp height. If species have similar tooth widths but different cusp heights then the apical angle of their dentine horns must also be different.

Table 4.40: Enamel thickness mesurements from buccal to lingual sections through the hypoconid and entoconid in lower second molars (M_2) compared with the mean values determined by Kay (1981)

Genus		E_m	c/e	k	m	q	s	$E_m/(c/e)$	E_m/k	E_m/m	E_m/q	E_m/s
Pan	Mean	0.95	0.79	0.92	0.96	1.02	0.89	1.20	1.03	0.99	0.93	1.07
	Min	-	0.65	0.77	0.86	0.71	0.83	-	-	-	-	-
	Max	-	0.86	1.04	1.06	1.18	0.94	-	-	-	-	-
Gorilla	Mean	1.14	0.98	0.93	0.95	1.49	1.17	1.16	1.23	1.20	0.77	0.97
	Min	-	0.69	0.71	0.77	1.18	0.88	-	-	-	-	-
	Max	-	1.24	1.12	1.16	1.71	1.42	-	-	-	-	-
Homo	Mean	-	1.23	1.26	1.29	1.83	1.56	-	-	-	-	-
	Min	-	1.17	1.18	1.24	1.71	1.47	-	-	-	-	-
	Max	-	1.29	1.33	1.33	1.95	1.65	-	-	-	-	-
Pongo	Mean	1.49	1.08	1.10	1.20	1.84	1.42	1.38	1.35	1.24	0.81	1.05
	Min	-	1.05	1.06	1.14	1.75	1.26	-	-	-	-	-
	Max	-	1.11	1.18	1.27	1.95	1.59	-	-	-	-	-

Notes: E_m is taken from Table 1 in Kay (1981)

c/e, k and m are my enamel thickness measurements as shown in Figures 4.1 and 4.2

q and s are enamel thickness measurements as shown in Figure 4.26

The last five columns indicate how precisely, and most importantly how consistently Kay's (1981) measurement of enamel thickness corresponds with direct measurements.

using oblique measurements of enamel thickness (e.g. Kay, 1981) do not necessarily invalidate the method. However, my results do not support the assumption that the angle of the dentine horns is constant across even closely related species. The assumption of a constant angle of the wear facet plane is equally suspect, Grine (1981) has shown that wear facets develop at different angles to the crown in Paranthropus and Australopithecus.

The bias due to dentine horn configuration and the shortcomings of single linear measurements of enamel thickness (Tables 4.27 - 4.35) give rise to doubts about the reliability of Kay's (1981) results. This means that the results presented cannot be used to extend the directly measured data reported here to a wider range of primates. The only other published data are those of Gantt (1977) taken on cut sections. A comparison of the actual figures presented by Gantt (1977, Appendix) with the data which I am presenting here reveals a surprising discrepancy between measurements apparantly taken, and certainly defined, in the same way (Figures 4.1 and 4.2). A comparison of the mean values provided by Gantt (1977) with the range of values which were encountered in the present work is shown in Table 4.41. Remarkably 59 of the mean values of the data presented by Gantt (1977) lie above the ranges of values encountered in the present study (which are usually based on larger samples, Table 4.41); two of Gantt's mean values lie below the range that I have observed; and only 25 of Gantt's (1977) mean values fall within the range of my observed values.

Table 4.41: Comparison of mean values obtained by Gantt (1977) with the range of values observed in this work.

Genus	Tooth		f	g	h	i	j	k	l	m	n
Pan	M^2	Gantt (1977) sample	2	-	2	2	2	2	2	2	2
		Gantt (1977) mean	0.76	-	0.74	0.75	0.84	0.88	1.07	1.00	1.40
		My results minimum	0.47		0.63	0.57	0.65	0.59	0.61	0.60	0.97
		My results maximum	0.59		0.73	0.70	0.71	0.91	0.98	0.94	0.98
Pan	M_1	Gantt (1977) sample	-	-	1	1	1	1	1	1	1
		Gantt (1977) mean	-	-	0.76	0.57	0.63	0.98	0.97	1.25	0.97
		My results minimum			0.52	0.51	0.47	0.68	0.57	0.74	0.57
		My results maximum			0.74	0.60	0.71	0.85	0.90	0.97	0.92
Pan	M_2	Gantt (1977) sample	4	4	7	6	7	7	7	7	7
		Gantt (1977) mean	1.17	0.88	0.85	0.84	0.87	1.10	0.99	1.22	1.09
		My results minimum	0.41	0.47	0.58	0.48	0.59	0.53	0.72	0.53	0.72
		My results maximum	0.83	0.74	0.81	0.81	0.94	0.94	0.98	1.03	0.98
Gorilla	M^2	Gantt (1977) sample	2	3	3	3	3	2	3	2	3
		Gantt (1977) mean	1.19	1.35	1.15	1.17	0.98	1.11	1.30	1.15	1.46
		My results minimum	0.88	1.06	0.77	0.61	0.53	0.90	0.78	0.90	0.85
		My results maximum	1.06	1.12	1.06	0.86	0.71	1.05	0.99	1.09	1.06
Gorilla	M_1	Gantt (1977) sample	2	3	3	3	4	4	4	4	4
		Gantt (1977) mean	1.05	0.99	0.91	1.04	0.97	1.17	1.00	1.37	1.06
		My results minimum	0.47	0.77	0.83	0.57	0.65	0.83	0.83	0.88	0.83
		My results maximum	0.67	0.88	0.94	1.16	1.14	0.85	1.04	0.88	1.30
Gorilla	M_2	Gantt (1977) sample	5	4	7	5	5	6	5	7	5
		Gantt (1977) mean	1.19	1.03	1.11	1.05	1.04	1.30	1.07	1.54	1.14
		My results minimum	0.59	0.71	0.64	0.60	0.67	0.93	0.83	1.01	0.83
		My results maximum	0.94	1.09	1.30	1.12	1.42	1.32	1.01	1.53	1.03
Homo	M^2	Gantt (1977) sample	1	1	-	-	-	1	1	-	-
		Gantt (1977) mean	2.02	2.09	-	-	-	1.12	1.24	-	-
		My results minimum	0.94	1.06				0.84	0.91		
		My results maximum	1.65	2.06				1.38	2.24		
Homo	M_1	Gantt (1977) sample	1	1	-	-	1	1	1	1	1
		Gantt (1977) mean	1.97	1.87	-	-	1 12	1.62	1.40	1.65	1.28
		My results minimum	0.77	1.00			0.59	1.18	0.94	1.39	0.97
		My results maximum	1.67	2.18			1.06	1.58	1.14	1.70	1.14
Homo	M_2	Gantt (1977) sample	1	1	-	-	1	1	1	1	-
		Gantt (1977) mean	2.00	1.80	-	-	1.36	1.40	1.23	2.18	-
		My results minimum	1.12	1.36			0.59	1.53	1.10	1.56	
		My results maximum	1.77	1.53			1.18	1.79	1.16	1.86	
Pongo	M^2	Gantt (1977) sample	1	1	1	1	1	1	1	1	1
		Gantt (1977) mean	1.32	1.52	1.28	1.34	1.12	1.17	1.35	1.32	1.67
		My results minimum	0.94	1.24	1.06	1.11	1.18	1.04	1.23	1.06	1.34
		My results maximum	1.12	1.36	1.22	1.29	1.30	1.06	1.57	1.11	1.63
Pongo	M_1	Gantt (1977) sample	1	1	2	1	2	1	2	2	1
		Gantt (1977) mean	1.57	1.30	1.11	1.11	1.15	1.18	1.11	1.58	1.07
		My results minimum	0.77	0.83	1.04	0.74	0.83	1.05	0.92	1.42	0.92
		My results maximum	1.06	1.02	1.46	1.39	1.47	1.18	1.12	1.53	1.14

Notes: Enamel thickness measurements (f) - (n) are as shown in Figure 4.2. Data from Gantt (1977) were compiled from Appendix A (Gantt, 1977). Observed minimum/maximum are the results from this research. Underlined values of means from Gantt (1977) lie above the range of observations reported in the present work, overlined values lie below the range found in the present work.

There are two possible explanations for this discrepancy: firstly the samples which Gantt (1977) used may be quite different in enamel thickness compared to the larger samples which I have used, if this is the case then the species ranges would be further extended for the linear measurements; secondly it may be the case that his set of measurements has been taken differently or possibly on sections which have been taken so as to reveal oblique enamel thicknesses. I have argued above that radial measurements of enamel thickness cannot be underestimated due to technical errors, but oblique sections exaggerate the apparant thickness of the enamel. I have observed that measurements of similar magnitude to those of Gantt (1977) may easily be found on a face which is not sampling the maximum diameter of the dentine horns (see Figures 4.12a&b, 4.13a,b&j, 4.14a), and it seems possible that since Gantt's (1977) measurements are consistently above or at the upper end of the measurements which I have presented that obliquity may have distorted his data. It must be stressed however that it is possible that real differences have been encountered. Whatever the reason it is clear that the data presented here cannot be combined with the data provided by Gantt (1977).

The data recorded by Gantt (1977) and Kay (1981) are consistent with the results presented here in terms of the ranking of relative enamel thickness. This means that it may not be unreasonable to use their results for other catarrhines in order to make broad statements about the evolution of thick enamel. On the basis of Gantt's (1977) data, it seems clear that a large proportion of cercopithecoids have thin enamel, although Kay's (1981) estimates of enamel thickness indicate

that there may be thick enamelled monkey species. This situation, and especially the position of the gibbons, needs to be clarified by the preparation of sections for a sample of teeth for these species.

I have drawn attention to the fact that Simons' (1976) method for dividing teeth into "thick" and "thin" enamelled categories is not consistent with the metrical data presented here. Firstly, it is not the case the Homo has a relatively flat dentine surface although some thick enamelled hominoids (Pongo, Sivapithecus) do. Secondly, Pongo has intermediate/thick enamel although its dentine exposure pattern is the "thin enamelled" one as defined by Simons (1976). This is particularly surprising as Pongo has in fact got a relatively flat dentine surface. In fact the dentine exposure pattern in Pongo is somewhat different to that in Pan and Gorilla in that dentine is only exposed on each cusp separately when the cusps are well worn down, whereas in the African apes the dentine is exposed when the cusps are still very projecting.

My observations of human teeth suggest that they sometimes show the "thin enamelled" wear pattern described by Simons (1976). The "thick enamelled" wear pattern is best exhibited in Sivapithecus, Kenyapithecus, and also in the Plio-Pleistocene hominids Australopithecus and Paranthropus. The latter species are often used by palaeoanthropologists as the human type, but they appear to be different in many respects from Homo in terms of enamel thickness. Bernard Wood (personal communication) has noted that some specimens of Homo from Koobi Fora exhibit the "thin enamelled" wear pattern. I

interpret these discrepancies to mean that while the pattern of dental wear said to characterise "thick enamelled" species certainly indicates that the species showing it has thick enamel, the "thin enamelled" wear pattern may be found in species with either intermediate/thick or thin enamel. In other words any species which exhibits the "thick enamelled" wear pattern can be safety identified as having thick enamel, but species which do not exhibit this pattern may not necessarily be regarded as being thin enamelled. Pongo does have slightly thinner enamel relative to tooth size than do Homo and Sivapithecus (Figures 4.17 - 4.24, Table 4.26). This suggests that there is a very sharp cut off point, between species with intermediate/thick enamel which exhibit the "thin enamelled" wear pattern (e.g. Pongo and sometimes Homo) and species with thick enamel which exhibit the "thick enamelled" wear pattern (e.g. Sivapithecus, Kenyapithecus, Australopithecus and Paranthropus). The species exhibiting the "thick enamelled" wear pattern have the maximum thickness of enamel observed in the present work in conjunction with relatively flat dentine surfaces (Sivapithecus), Pongo has the flat dentine surface and intermediate/thick enamel, but exhibits the "thin enamelled" wear pattern, Homo has the maximum observed thickness of enamel with high dentine horns and sometimes shows the "thin enamelled" wear pattern, Pan and Gorilla have thin enamel, high dentine horns and, as expected, show the "thin enamelled" wear pattern. It seems likely that Australopithecus and Paranthropus have high dentine horns and they must therefore have very thick enamel since they exhibit the "thick enamelled" wear pattern. Kenyapithecus and Sivapithecus meteai have the "thick enamelled" wear pattern

so they must have thick enamel, but only direct observations can resolve the question of the height of their dentine horns.

In view of the problems raised by the wear patterns which reflect the fact that enamel-dentine junction morphology as well as enamel thickness is involved in determining the pattern of dentine exposure it is unwise and misleading to use these patterns to make absolute distinctions with regard to enamel thickness. The observation of dentine exposure patterns permits the recognition of some species which are thick enamelled, but is unable to reliably sort other species which have intermediate/thick enamel (e.g. Pongo) from species which have thin enamel (e.g. Pan and Gorilla). I believe that the use of the terms "thick enamelled" and "thin enamelled" wear pattern have no validity and that their continued use will maintain confusion unnecessarily when metrical data have established clear and reliable results. The dentine exposure patterns are what we use to define the "thick enamelled" and "thin enamelled" wear patterns, these have been shown to be invalid definitions. The dentine exposure patterns are however of considerable interest. I propose that the exposure patterns be renamed as dentine fusion for the species where dentine spots combine together before dentine has been exposed on every cusp - previously known as the "thick enamelled" wear pattern (Simons, 1976) and dentine separation for the species in which dentine is exposed on four or five cusps separately at one time before any spots join together (previously known as the "thin-enamelled" wear pattern (Simons, 1976)). These terms are useful and descriptive and avoid the confusion caused by saying that a species is "thin enamelled" (from

its wear) when metrical study may show that it has intermediate/thick enamel (as was the case with Pongo). It seems likely on the basis of the present work that all species showing dentine fusion wear will have thick enamel. Dentine separation wear will combine species with thin enamel, intermediate/thin enamel and intermediate/thick enamel.

V. THE EVOLUTIONARY SIGNIFICANCE OF ENAMEL THICKNESS

The evidence from the sample reported here is that Pan and Gorilla have thin enamel (mean of relative enamel thickness index between 8.90 and 11.30), Pongo has intermediate/thick enamel (mean of relative enamel thickness index between 14.65 and 17.25), Homo and Sivapithecus have thick enamel (mean of relative enamel thickness index between 17.70 and 26.20). No species with intermediate/thin enamel (mean of relative enamel thickness index between 11.30 and 14.65) were documented. A single specimen of Hylobates has thin enamel (relative enamel thickness index 11.02). The thinner enamel in Pongo compared to Homo and Sivapithecus explains why its dentine exposure pattern is the dentine separation type and superficially similar to that of the African apes.

The evolutionary significance of these findings greatly depends on the evolutionary polarity of enamel thickness. Outside of the great ape and human clade and the single Hylobates specimen for which I have provided data, the only evidence on enamel thickness comes from observations of dentine exposure patterns (Simons, 1976) or from the data of Gantt (1977) and Kay (1981). I have indicated doubt as to the accuracy of these data although they produce similar rankings for relative enamel thickness in the great ape and human clade. These data seem to convincingly identify the primitive state for the Primates clade, the anthropoid clade and the catarrhine clade as thin enamel. The

thin enamel in Hylobates reported here agrees with the data of Gantt (1977) and Kay (1981) and is most parsimoniously interpreted to mean that thin enamel is the primitive condition for the hominoid clade. Observations of the dentine exposure patterns confirms that dentine separation wear predominates in Primates. This does not rule out the possibility that some species have intermediate/thick enamel as does Pongo, but it does not contradict the general findings of Gantt (1977) and Kay (1981) which suggest than thin enamel is the most commonly found state in Primates. Kay (1981) suggests that a number of cercopithecoid and platyrrhine species may have relatively thick enamel, as did Jolly (1970b) for Hadropithecus. This would not influence the conclusions regarding the evolutionary polarity of enamel thickness, but may provide useful examples of parallel evolution which may help to provide an explanation of the functional significance of thick enamel (see Chapter 6).

The evidence therefore is that thin enamel is the primitive condition of the Hominoidea. The possession of thick enamel by Homo and of intermediate/thick enamel by Pongo and of thin enamel by both of the African apes raises a number of possibilities for the ancestral condition for the great ape and human clade; firstly thin enamel could be the primitive condition in which case either enamel has thickened by parallel evolution in the Pongo clade and in the Homo clade, but to a greater extent in the Homo clade, or these two genera form a sister group and thickening enamel is a character defining the Homo/Pongo clade.

This latter possibility has been rejected as unlikely in the face of comparative anatomical and molecular evidence (see Chapter 2); secondly intermediate/thick enamel could be the ancestral condition for the great ape and human clade. In this case Pongo would have retained its enamel thickness from the common ancestor of the great ape and human clade, Pan and Gorilla would have secondarily reduced enamel thickness and Homo or the common ancestor of the African apes and man would have thick enamel as a derived character; thirdly the common ancestor of the great ape and human clade could have had thick enamel in which case Pongo would have secondarily reduced its enamel thickness slightly, and the African apes would share a derived character of considerably reduced enamel thickness, Homo would retain the primitive condition from the ancestor of the great ape and human clade.

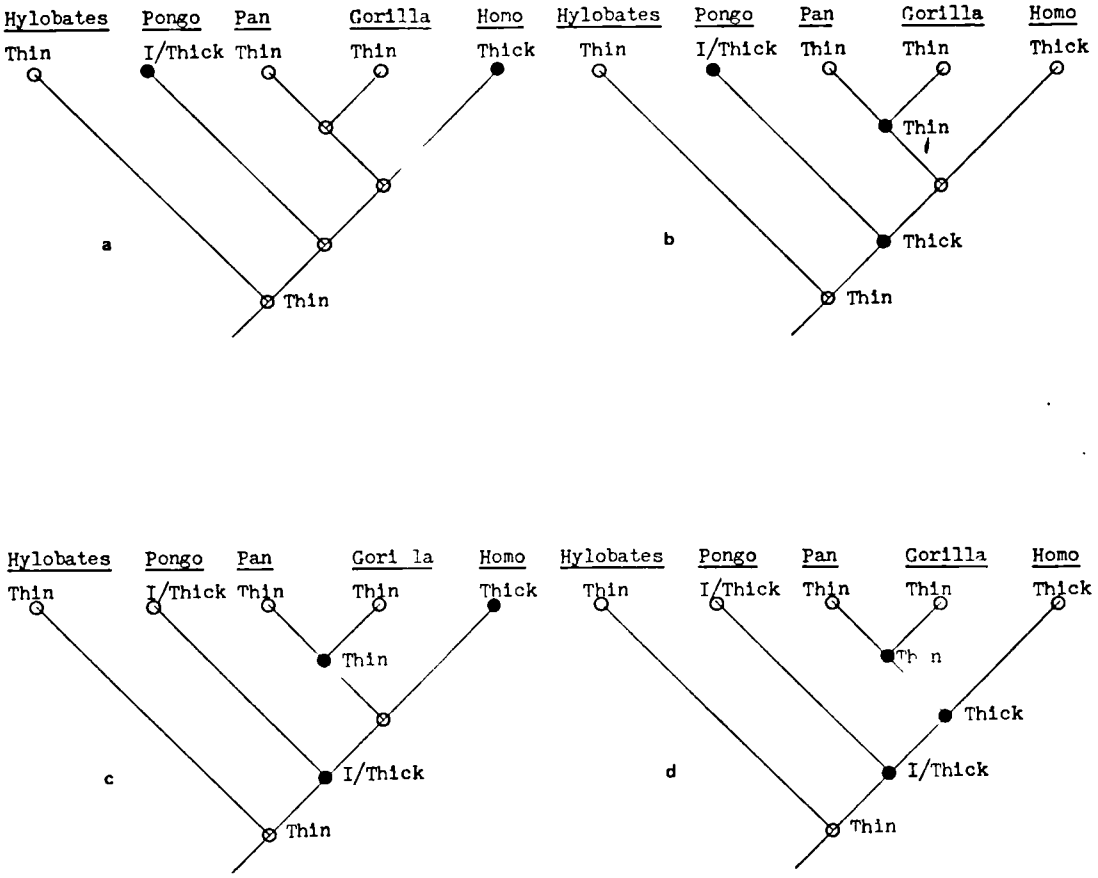
The most parsimonious interpretation for the condition of enamel thickness for the common ancestor of the African apes is that it had thin enamel. The common ancestor of the African apes and man gives rise to species with thin enamel and thick enamel, either thick enamel or thin enamel would be the most parsimonious condition in the common ancestor of the African apes and man as this would require change from the ancestral condition in only one clade from the common ancestor. If thin enamel were the primitive condition for the common ancestor of the African apes and man then parsimony would favour thin enamel as the condition in the common ancestor of the great ape and human clade. If thick enamel were the condition in the common ancestor of the

African ape and human clade then parsimony would suggest either thick or intermediate/thick enamel as the condition in the common ancestor of the great ape and human clade.

Four of the more parsimonious interpretations of the enamel thickness data and evolutionary polarity are shown in Figure 4.29. The position of Sivapithecus determined solely from enamel thickness would vary according to the resolution of the question of morphocline polarity of enamel thickness in great ape and human evolution. If thin enamel were the condition in the common ancestor of the great ape and human clade then the most parsimonious situation would be that thickened enamel had evolved in parallel in the Pongo and in the hominid clades and to a greater extent in the hominid clade (Figure 4.29a). If this were the case then the enamel thickness data in isolation would make Sivapithecus a hominid. Any other interpretation would falsify the recognised morphocline polarity shown in Figure 4.29a.

If thick enamel were the condition in the common ancestor of the great ape and human clade then Pongo would have an autapomorphic character of slightly reduced enamel thickness, Pan and Gorilla would share a derived character of considerably reduced enamel thickness. This interpretation would therefore require two evolutionary reversals by parallel evolution within the great ape and human clade. If this interpreation of morphocline polarity were accepted then the position of Sivapithecus could not be determined on the basis of its enamel thickness. It could

Figure 4.29: Four possible interpretations of the distribution of enamel thickness categories in extant hominoids.



Notes: O = character state retained from previous node

● = character state derived with respect to the previous node.

belong to any part of the hominoid clade subsequent to the separation of the Hylobates clade, but it could not belong to Pan and Gorilla clade. In other words if polarity is as shown in Figure 4.29b then a species with thick enamel, used as a character in isolation, could be a primitive member of the great ape and human clade prior to the first cladogenic event (the separation of Pongo), or it could be an early member of the Pongo clade prior to the secondary reduction in enamel thickness in modern Pongo. Alternatively it could be a primitive member of the African ape and human clade prior to the separation of the African ape clade from the hominind clade, or it could be an early member of the African ape clade prior to the secondary reduction of enamel thickness which had been achieved by the stage where Pan and Gorilla shared their last common ancestor, finally a species with thick enamel could be a hominid.

If the common ancestor of the great ape and human clade had intermediate/thick enamel then two equally parsimonious character states for the common ancestor of the African ape and human clade exist (Figure 4.29c & d). In the case shown in Figure 4.29c, with the common ancestor of the African ape and human clade having intermediate/thick enamel, then a species with thick enamel would have to be a hominid. It is equally parsimonious to interpret the common ancestor of the African apes and man as having thick enamel (Figure 4.29d), in this case a species with thick enamel could be either a hominid, or an early member of the African ape clade, or an early member of the African ape and

human clade prior to the branching of the human clade from the African apes clade but subsequent to the branching of the Pongo clade from the African ape and human clade. In other words only the interpretation of thick enamel as the condition in the common ancestor of the great apes and man would allow a species with thick enamel to be related to the orang-utan, any other primitive state for the great ape and human clade would mean that a species with thick enamel belonged to some part of the African ape and human clade, but never to the Pan and Gorilla clade.

The four possibilities considered the most parsimonious (shown in Figure 4.29) are testable. A necessary consequence of the interpretation of thick enamel being the condition in the common ancestor of the great ape and human clade (i.e. the primitive condition for members of the great ape and human clade) is that Pan and Gorilla and Pongo have undergone an evolutionary reversal and secondarily reduced their enamel thickness, to a far greater extent in the African apes than in Pongo. The thickness of enamel is the product of the length of time over which the tooth is formed and the mean daily formation rate. There are therefore two routes by which enamel thickness could be secondarily reduced; firstly by reducing the total period over which the teeth are formed (which seems unlikely as this would have many consequences beyond reducing enamel thickness); secondly enamel thickness could be reduced by slowing down the daily rate of formation for part or all of the period during which the tooth is formed. Secondarily reduced enamel should therefore be

detectable by microstructural analysis by observation of incremental features. If the common ancestor of the great ape and human clade had intermediate/thick enamel then Pongo would not have secondarily reduced enamel but the African apes would. The degree to which secondarily reduced enamel occurred would permit the recognition as to whether thick enamel or intermediate/thick enamel was the condition in the common ancestor of the African ape and human clade (Figure 4.29c & d). If thin enamel were the primitive condition in the common ancestor of the great ape and human clade then Pan and Gorilla would not have secondarily reduced enamel thickness and neither would Pongo (Figure 4.29a).

The evolutionary polarity of enamel thickness within the Hominoidea is therefore best determined by microstructural analysis as it cannot be definitely determined on the basis of the distribution of thick, intermediate/thick and thin enamel in hominoid species. The determination of the microstructural evidence regarding the polarity of enamel thickness changes in hominoid evolution forms the major component of Chapter 5. The microstructural evidence and the relative enamel thickness data are combined in Chapter 6 to determine the evolutionary polarity of enamel thickness in hominoid evolution.

VI. CONCLUSIONS

1) Enamel thickness has been an important character in the determination of the relationships of the later Miocene hominoids. Thick enamel has often been considered to be a derived character of the hominid clade.

2) Non-destructive methods for the determination of enamel thickness (Simons, 1976; Kay, 1981) are shown to be unreliable in the case of dentine exposure analysis, and of uncertain relationship to direct measurements of enamel thickness in the case of Kay's (1981) method.

3) Enamel thickness shows no clear intraspecific relationship to size in the four species studied.

4) Enamel thickness can be summarised by a single measurement of average enamel thickness c/e (Figure 4.1), the area of the enamel cap exposed in a section divided by the length of the enamel-dentine junction over which the enamel has formed.

5) Single linear measurements of enamel thickness (e.g. Gantt, 1977) are poor approximators of average enamel thickness.

6) Kay (1981) and Gantt (1977) have shown the large anthropoid species tend to have thicker enamel than do smaller anthropoids, but this can be allowed for by scaling the enamel thickness by tooth size (body size).

7) Dental estimates of body size for comparison with enamel thickness should ideally exclude any enamel component, ruling out any absolute dimensions of the tooth crown. Measurements of the dentine, cementum and pulp dimensions of the teeth are shown to be related to body size within the great ape and human clade in a similar, or more linear fashion, than are measurements of crown size. The square root of dentine area (b, Figure 4.1) has been used to produce an index of relative enamel thickness scaled for size. $\frac{(c/e)}{\sqrt{b}} \times 100$

8) Four categories of relative enamel thickness are metrically defined: thin enamel (mean values of relative enamel thickness between 8.90 and 11.30), intermediate/thin enamel (mean values of relative enamel thickness between 11.30 and 14.65), intermediate/thick enamel (mean values of relative enamel thickness between 14.65 and 17.25) and thick enamel (mean values of relative enamel thickness between 17.70 and 26.20).

9) Thin enamel is found in Pan (8.90 - 11.30), Gorilla (9.15 - 10.93) and probably Hylobates (11.02), intermediate/thick enamel is found in Pongo (14.65 - 17.21) and thick enamel is found in Homo (18.58 - 26.12). The values above are the 95% confidence limits of the means. No species with intermediate/thin enamel have been encountered.

10) Sivapithecus specimens, which provide the first published data on directly measured enamel thickness in three fossil species, have thick enamel (17.73 - 21.69).

11) Thin enamel is almost certainly the primitive condition for the Hominoidea.

12) The condition of enamel thickness for the common ancestor of the great ape and human clade cannot be reliably determined from the distribution of thin, intermediate/thick and thick enamel within this clade. The evidence of enamel thickness concerning the relationships of the later Miocene hominoids can only be reliably used if the cellular mechanisms by which the thickness has developed are understood. These will be discussed in the next chapter.

CHAPTER 5

ENAMEL MICROSTRUCTURE IN EXTANT AND EXTINCT HOMINOIDEA

I. INTRODUCTION

It has recently been suggested that examination of enamel prism cross sectional shape provides significant information related to the taxonomy of extant and extinct Hominoidea. In particular, it has been suggested that different prism packing patterns exist within the Hominoidea and that these can be used to differentiate between man's family, Hominidae, and the great apes (Gantt et al, 1977), although Vrba and Grine (1978a; 1978b) disagree with this conclusion. There is obviously considerable potential interest in the study of enamel prism packing patterns, and enamel microstructure in general, in fossil primates because enamel is the only tissue which can remain essentially unchanged by the processes of fossilization, as it is almost completely mineralized *in vivo*.

For the purposes of the present work there are three major areas of interest. Firstly, Gantt et al (1977) specifically addressed the taxomonic affinities of *Ramapithecus* on the basis of its enamel prism packing pattern. If a distinction exists between the enamel microstructure in members of the human clade and the non-hominid hominoids this would be of great interest in assessing the phylogenetic affinities of the later Miocene hominoids. In particluar it might provide a way to assess the position of *Sivapithecus* (including "*Rampithecus*") (Kay, 1982b; Martin and Andrews, 1982). Secondly, any difference in enamel structure between species would complicate direct comparisons of enamel thicknesses, unless it could be demonstrated that the structural differences had no functional

consequences, which seems unlikely. Thirdly, microscopical examination of enamel structure offers the opportunity to directly study the cell and developmental biology of the formation of enamel. This will allow enamel dimensions to be considered in the light of knowledge concerning the mechanism by which the thickness has developed. In particular it should permit the recognition of enamel which is thick as a result of lengthened period of formation from enamel which is thick as a result of increased daily secretion rate, a difference that could have phylogenetic implications.

There is a high degree of agreement regarding the structure of enamel in Homo sapiens, but there is less concensus regarding the non-human Primates. This chapter attempts to address the key question (for the assessment of the relationships and adaptations of the later Miocene hominoids), whether differences in enamel microstructure do exist within the Hominoidea. The answer to this question will either provide a valuable criterion for assessing taxonomic affinities or will allow much greater confidence regarding the comparison of enamel thicknesses between species (when it is known that structurally homologous thicknesses are being compared).

1. Structure and development of dental enamel

The structure and development of enamel is controlled genetically through the pattern of behaviour, movement and secretion of the ameloblasts. Enamel is a composite material comprised of two phases; a mineral phase and an organic phase. The mineral phase, an apatitic calcium phosphate, is the major component and accounts for the hardness of the tissue. The properties of the mineral phase are modulated dramatically because it is divided into approximately 0.05 μm diameter whiskers or fibres known as "crystals". The crystals are cemented together by the organic phase, which is a complex protein polymer. The composite resists brittle fracture far better than does crystalline apatite alone (Boyde, 1976).

The long, thin crystals that compose the major phase in enamel are oriented roughly perpendicular to the tooth surface. During tooth development these crystals grow in a gel of protein matrix which disappears to a large extent as the crystals grow within it. Eventually the protein matrix takes the form of extremely thin layers which both bond and separate the enamel crystals.

The orientation of the enamel crystals results from their tendency to grow perpendicularly to the surface from which they develop. The developing surface is not simply flat, but is pitted by the secretary pole processes of the ameloblasts to form the Tomes' process pits. By visualizing crystals growing perpendicular to the pitted surface it is clear that discontinuities in crystal orientation develop at the

sharp concavities where the floors meet the walls of these pits. These discontinuities in crystal orientation are known as prism boundaries or junctions: they define partially separated bundles of enamel crystals a few microns in diameter called enamel prisms. The prism boundary locations acquire a more concentrated organic matrix during mineralisation, and in the adult tissue are distinguished by the name prism sheaths. Enamel is not, however, completely subdivided into prismatic units because the discontinuities (prism sheaths or boundaries) are not usually continuous with one another (see Figure 5.1). This has considerable implications when considering the ability of enamel to resist fracture.

The separation into prisms is exaggerated in many studies of the mature tissue as an artefact of drying and cracking or of etching. Acid etchants dissolve a part of the enamel crystals to produce an acid calcium phosphate salt which is relatively insoluble at low pH. This salt deposits around the prism boundary discontinuity (gap or crack) which is thus enlarged. Later in the dissolution process, the new (salt) phase remains proud of the etched surface: on air drying the gap collapses so that acid etched enamel shows a modified and continuous structure which was not present before etching. This artefact is most severe when etching heavily (i.e. at high concentrations or for long periods) (e.g. Gantt et al, 1977; Vrba and Grine, 1978a, 1978b).

It is necessary to use some kind of etchant in preparing mature enamel for scanning electron microscopy (SEM) because most methods of

sampling the subsurface enamel involve some kind of mechanical tissue removal (grinding, cutting etc) which "smears" the enamel, obscuring the structure. Etching removes this smear and reveals the underlying structure, but may also modify its appearance. Artefacts of this kind can be minimised by followed the recommendations of Boyde et al (1978).

In the great majority of mammals, the enamel prisms are arranged into groups or zones of prisms which decussate i.e. pursue oppositely oriented (sinusoidal) courses in their passage from the enamel-dentine junction to the surface of the tooth, making the so-called Hunter-Schreger band pattern. The overall path of a prism from the enamel-dentine junction to the tooth surface is a flattened helix.

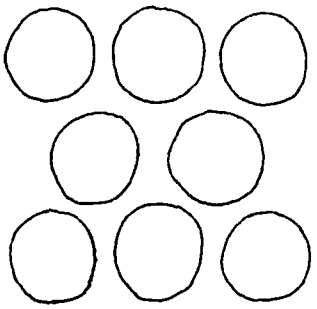
In addition to this factor the prisms get fatter and thinner along their length, their tail portions (or interprismatic regions) expanding at the expense of the head, and vice versa. These varicosities are called cross striations and the length from one periodic feature to the next almost certainly represents 24 hours of enamel development (Boyde and Martin, 1983). This is a particularly useful feature for illuminating the cellular mechansism by which enamel thickness is produced. The cross striations are sometimes exaggerated to produce incremental lines known as the brown striae of Retzius (1837). These incremental lines correspond with major constrictions in the diameter of the prism "head", due to enamel development slowing down more than usual. The mean crystal orientation changes dramatically in the plane of an incremental line

to become more cervically directed.

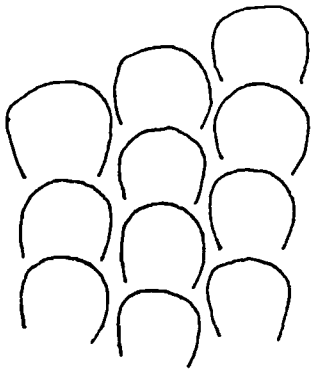
Boyde (1964) defined three basic patterns which described enamel prism cross sectional shape based on a study of the developing enamel surface in a wide variety of mammals. These three patterns are not entirely distinct and some intermediate forms may be found. However, the majority of prisms in one zone of enamel in one species will conform most closely with one particular type. The depth at which the enamel is sampled is of considerable significance in this regard, and requires both control and quantification, because a single prism can show various patterns at different portions of its length. The three major packing patterns and some subsidiary patterns are shown in Figure 5.1. Boyde (1969a) has shown that Pattern 2 enamel is formed by ameloblasts with a small cross sectional area, Pattern 1 by ameloblasts with a medium size cross sectional area and Pattern 3 by ameloblasts with a large cross sectional area.

Pattern 1 is the commonest type found in Sirenia, Cetacea and Chiroptera but is often also found in the very deep enamel, near the enamel-dentine junction, and in the enamel close to the tooth surface in other Orders. Pattern 2 is commonly found in the Lagomorpha, Artiodactyla and the Perissodactyla. Strong decussation of the prisms in the Rodentia interferes with the identification of a basically Pattern 2 arrangement. Pattern 3 enamel is commonly found in Carnivora, Pinnipedia and Proboscidea (Boyde, 1964).

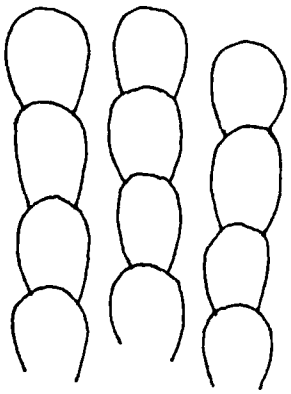
Figure 5.1: Enamel prism packing patterns defined by Boyde (1964). This figure is redrawn from Figure 1 in Boyde (1964). The enamel prism packing patterns which Boyde (1964) defined on the basis of an extensive survey of developing enamel surfaces in extant mammals are used throughout this chapter, and in Chapter 6. The prism patterns are not completely exclusive, but in the majority of mammals one or other of the patterns predominates.



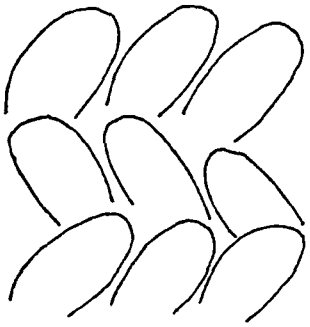
Pattern 1



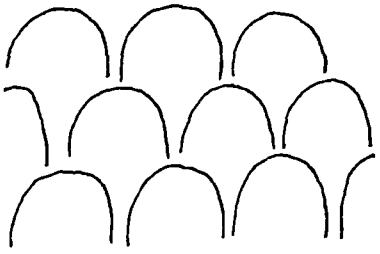
Pattern 2



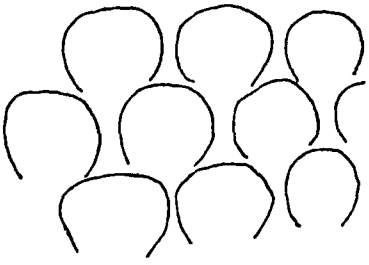
Pattern 2A



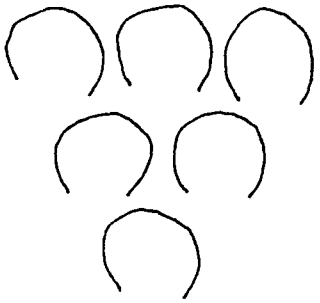
Pattern 2B



Pattern 3



Pattern 3B



Pattern 3C

2. Primate enamel structure

The first systematic survey of primate enamels was carried out by Carter (1922) and concentrated on the presence of tubules, continuous with the dentine tubules, in enamel, which he found to have the highest incidence in Prosimians. There has been little subsequent interest in enamel tubules in this regard, probably because there is, for example, a high incidence of enamel tubules in human enamel, but these tubules are so fine that they require electron microscopical techniques for their demonstration (Boyde and Lester, 1967). The same is true for gibbon enamel (Boyde and Martin, 1983). There seems little hope therefore that enamel tubules will be of use in taxonomic studies within the Order Primates.

Prism decussation is an aspect of enamel structure which has proven to be of considerable significance in distinguishing among taxonomic groupings in the Rodentia (Tomes, 1850; Korvenkontio, 1934; Boyde, 1978). Surveys of decussation patterns in primate enamels have been conducted by Kawai (1955) and Shellis and Poole (1977). Kawai's data would not suggest that decussation was a useful means of distinguishing among possibly different types of primate enamels, decussation being easily recognised in all of the genera studied except Alouatta and Ateles, in which it was poorly marked, and Tarsius in which no decussation was observed. Shellis and Poole (1977) however, reported that there was no decussation in Gorilla enamel and that decussation was poorly marked in Callitricidae and Prosimii. In view of these indications, and especially the reported situation for

Gorilla, prism decussation deserves further attention in studies of primate enamel microstructure.

Present day attention is focused on the cross sectional shape of the prisms as the most interesting feature of enamel structure for taxonomic studies, probably because it is the feature most easily studied with least damage necessitated. This feature has been extensively studied in human enamel and all descriptions since Nasmyth (1839) and Smreker (1905) have given the shape of human enamel prisms as that described as Pattern 3 by Boyde (1964) (Figure 5.1). In the first comprehensive comparative study of enamel prisms in the different mammalian Orders Shobusawa (1952) referred to the Pattern 3 organisation as "the primate type" although it is unclear which species he sampled. Boyde (1964) concluded that Pattern 3 prisms were found in Man; Pattern 2 was frequent in Macaca mulatta and Boyde (1966) found Pattern 1 enamel in a lemur. This distribution suggests that enamel prism packing patterns may be of considerable value for taxonomy in Primates as no other Order has yet been reported to exhibit each of the three major enamel prism packing patterns. However, Boyde (1964) noted that Patterns 1, 2, and 3 could be found in localised regions of both human and rhesus enamel. He found that Pattern 1 enamel is frequently located in a thin layer close to the enamel-dentine junction and, of potential interest with reference to the publications of Gantt et al (1977), Vrba and Grine (1978a,b) and of particular interest with reference to the publication of Gantt (1979), just deep to the surface of the tooth in many of the mammals he studied. These results demonstrate the necessity to document

enamel prism patterns in precise locations and at defined (and preferably measured) depths in order to avoid possible confusion resulting from the comparison of non-homologous regions of the enamel.

Recently, Gantt, Pilbeam and Steward (1977) reported on the SEM investigation of (heavily) acid etched enamel in Pan troglodytes, Gorilla gorilla, Pongo pygmaeus and Homo sapiens. They considered that the great apes have an enamel prism cross sectional shape which is consistently "circular or hexagonal", distinctively different from that of Homo sapiens which they described as showing a "keyhole" pattern. The circular pattern illustrated in Gantt et al (1977, Figure 2) corresponds with Pattern 1 as recognised by Boyde (1964) (see Figure 5.1). These authors' use of the term hexagonal can only be interpreted with reference to Gantt's later publication (Gantt, 1979); it is thus clear that his hexagonal type combines Pattern 3 (as shown in plate 5 of Gantt, 1979) and Pattern 2 (as shown in plates 6 and 7 of Gantt, 1979).

On the basis of the differences observed between the great apes and man, Gantt et al (1977) prepared a fossil specimen which they attributed to Ramapithecus punjabicus, using the same etching regime (vis, 0.5M HCl for 2.5 minutes on an unprepared true tooth surface) and concluded that it also showed a keyhole pattern and was therefore a hominid rather than an ape.

Vrba and Grine (1978a,b) disagreed with the conclusions of Gantt et al (1977) as they had found, using the same preparative method, that

Pattern 3 predominated in Pan troglogytes, Gorilla gorilla, Pongo pygmaeus as well as in Homo sapiens. They also confirmed the findings of Boyde (1964) that Patterns 1 and 2 could be found in localised areas of hominoid enamel. In spite of their conclusion that the enamel prism patterns are not significantly different within the group comprising the great apes and man, they applied the same preparative technique to specimens of Paranthropus and Australopithecus in order to examine possible differences in the etching procedure as applied to fossilized teeth (Grine, personal communication). They determined that both Paranthropus and Australopithecus showed a predominantly Pattern 3 organisation of their enamel prisms.

Shellis and Poole (1977) produced a comparative survey of the hard tissues of primates. They reported that (heavily) acid etched Pan and Gorilla enamel both showed mainly Pattern 3 morphology in the deep enamel. They noted that the surface prisms in Pan were often circular or spiral shaped, although this was not the case in Gorilla. They reported that prism decussation was slight in Gorilla but well marked in the inner two thirds of the enamel in Pan. In both genera they found that the outer enamel prisms were non-decussating. Shellis and Poole (1977) reported Pattern 3 prisms in Macaca and Papio and noted that in Macaca particularly these were often arranged in rows giving a superficial appearance of a Pattern 2 arrangement. Boyde (1964) has documented the enamel prism packing pattern in Macaca on the basis of developing surface material and showed that the arrangement is in fact

Pattern 2. It is clear from their discussion that Shellis and Poole (1977) are using a different definition of the prism packing pattern types than those developed by Boyde (1964). Using their own definition they recorded Pattern 3 enamel in Cebidae and reported Pattern 1 enamel in Callitrichidae and Prosimii. In all species examined Shellis and Poole (1977) reported cross striation repeat intervals of about 5 μm. In some species they found major striations at 10 μm intervals but in these cases fine striations were found midway between these major striations.

Boyde, Jones and Reynolds (1978) described a method for measuring the total depth of tissue removed and the local etch depth (localised relief resulting from differential etching). They investigated the effect of a variety of concentrations of HCl, H_3PO_4, lactic acid and EDTA and concluded that a 0.5% H_3PO_4 solution was a generally satisfactory reagent (a 0.5% H_3PO_4 solution made by diluting concentrated (88%) H_3PO_4 200-fold is 0.074M). Their measurements indicate that the etching regime used by Gantt et al (1977) and Vrba and Grine (1978a,b) (viz 0.5M HCl for 2.5 minutes) would remove 60-70 μm of enamel and cause a local etch depth of 2-3 μm. Sixty micrometers of enamel is certainly more than the usually reported values for the prism free superficial layer of enamel, but I have found that prism patterns which are not typical for the bulk of the enamel may be found in a relatively thick surface layer in Pan and Gorilla and to a lesser extent in Pongo (see Results section for more detailed information). To remove such a great thickness of enamel, as would be required to sample the deep enamel consistently, by the

etching regime of Gantt et al (1977), also used by Vrba and Grine (1978a,b) would render the prismatic structure viewed too subject to reprecipitation and drying artefacts to be reliably interpreted. It should be noted however that Vrba and Grine (1978a,b) produced results which are in agreement with the findings of Boyde and Martin (1982, 1983) for developing enamel.

The total etch rate for fresh human enamel with 0.5% H_3PO_4 is roughly 1 μm per minute. It should be noted that etch rates may be different in fossilised specimens. A high fluoride content reduces the etch rate while a high carbonate content may increase the etch rate compared to fresh enamel. I have found that etch times of 30 seconds to 120 seconds may be used with minimal artefact development. This regime does not remove sufficient tissue to cut through the prism free superficial layer even in human teeth and certainly not in species in which the outer layer of enamel has a prismatic structure which is not typical of the bulk of the enamel, so some kind of mechanical removal of tissue must be used.

Shellis and Poole (1977) used an etching regime (normal HCl for 10-20 seconds) which would remove about 15 μm of enamel. They sampled deeper enamel by cutting and polishing facets perpendicular to the long axis of the prisms. Gantt (1979, 1980, 1981) has recognised the problem of artefacts in the method which he previously used (Gantt, et al, 1977) and has followed the regime recommended by Boyde et al (1978), viz a 0.5% H_3PO_4 solution. He has used a diamond polisher to produce a facet on the tooth which samples the enamel at a number

of depths up to an underfinable maximum. Using this method Gantt (1979) has argued that the differences between ape and hominid enamel reported by Gantt et al (1977) are real, although he states that it may be necessary to repolish and re-etch the specimen several times before the "representative" pattern is observed (Gantt, 1979 p.494).

I have attempted to reproduce these results (see Results section of this chapter) but find that the method produces inconsistent results. A recently published paper by Gantt and Cring (1981) implicity retracts the position taken by Gantt (Gantt et al, 1977, Gantt 1979, 1981). They report that all Miocene hominoids sampled (Proconsul, Sivapithecus, Ramapithecus and Gigantopithecus) have a Pattern 3a prism packing pattern. They report that Homo and Australopithecus have a Pattern 3b arrangement. Although Gantt and Cring (1981) do not directly address the difference between these results and those previously described by Gantt et al (1977; Gantt 1979, 1981) they illustrate a Pongo specimen showing a Pattern 3a arrangement. Implicit in their discussion is the recognition that the great apes do have a Pattern 3 arrangement as stated by Vrba and Grine (1978a,b), and Shellis and Poole (1977).

I have recently examined the possible difference between enamel structure in Homo sapiens, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus and Hylobates lar on the basis of examination of the developing enamel surface in a joint study with Professor Alan Boyde (Boyde and Martin 1982, 1983). Erythrocebus patas and Macaca mulatta were included in this study to provide preliminary data on enamel

structure in Cercopithecidae. Boyde (1964) has shown that prism shape and decussation can be recognised from the shape and arrangement of Tomes' process pits in the surface of the developing tissue. We therefore felt that if there were significant differences to be found among primates, and particularly among Hominoidea, these would certainly be discovered from a study of developing material.

Boyde and Martin (1982) described a number of methods for preparing tooth germs for examination of the developing enamel surface. Essentially these involve drying the specimen by critical point drying or freeze drying in order to minimise the surface tension effects of drying. Cell debris which remains attached to the developing enamel surface tends to obscure the Tomes' process pits. The cell debris was therefore either dissolved prior to drying, or removed by oxygen plasma ashing after drying (Boyde and Martin, 1982). All of the methods for preparing the developing surface for SEM produced similar results which in turn could be easily related to the appearances seen in section by transmission electron microscopy (TEM) (Boyde and Martin, 1982). The relationships of crystals and prisms to the shape of the developing enamel surface (which for all practical purposes may be taken as the shape of the mineralizing front) has been described in detail by Boyde (1964, 1967, 1976).

The prism cross sectional shape can be determined by direct inspection of the developing enamel surface preparation by viewing with real time stereo TV-speed SEM with the sample attached to a stage providing rotation, tilts, X, Y and Z movements. It is then possible

to orient the specimen, by inspection, so that the continuous cuspal and lateral walls of the pits are viewed at grazing incidence: the sample is oriented such that the walls do not quite eclipse the floor. This true cross sectional view does not correspond exactly with the oblique cross-section revealed by the tooth-surface-parallel etching techniques described by Gantt et al (1977: Gantt, 1979, 1980, 1981; Gantt and Cring, 1981) and Vrba and Grine (1978a,b).

An extensive study of human material showed a great consistency between samples and Boyde and Martin (1982, 1983) were unable to discover any important differences between deciduous and permanent teeth, and between different sites on different tooth types. This result means that small samples of specimens from any species do not necessarily invalidate conclusions based on their study. However, I have determined that a small area on one sample, and at one depth within the MATURE tissue, CANNOT be taken to represent the range of variation to be expected within one tooth, never mind between different teeth within the same species. Boyde and Martin (1982, 1983) conclude that a survey of prism cross sections should cover several mm^2 of tissue sampled at various (preferably measured) depths from the tooth surface through to the enamel-dentine junction. The prism pattern which may be regarded as typical or representative of a species group is sampled in the deeper layers of enamel, not immediately subsurface.

I was able to determine that all of the hominoids sampled show a predominantly Pattern 3 organisation of their enamel in all developing

surface preparations. Localised areas of Pattern 2 and Pattern 1 enamel were often encountered. The reasons why Gantt et al (1977) preferentially sampled these areas are explained in the discussion section of this chapter. The developing enamel surface was examined in two species of cercopithecoid monkey, both of which showed predominantly Pattern 2 organisation with varying degrees of Pattern 1 enamel in localised areas. No Pattern 3 enamel was observed, in cercopithecoids, although the presence of localised zones would not be surprising. However, the enamel prism packing Pattern studies suggest that, if the results for Macaca mulatta and Erythrocebus patas apply to all cercopithecoids, then the Hominoidea can be reliably sorted from the Cercopithecoidea on the basis of enamel prism packing patterns observed in preparations of developing enamel surfaces (Boyde and Martin, 1982; 1983).

This review of the currently available data on enamel prism packing patterns indicates that all hominoids have the same arrangement of Tomes' process pits in the developing enamel surface. These preparations sample deep enamel and suggest that enamel structural patterns are unlikely to provide simple dichotomous patterns which would permit the recognition of hominid and non-hominid hominoids even when extensive surveys of the mature tissue are conducted. The results for the Cercopithecoidea, Platyrrhini and Strepsirrhini (Boyde and Martin, 1983) suggest that direct comparisons of enamel thickness between, for example, cercopithecoids and hominoids, will be complicated by structural differences between their enamels.

The aim of the present work is therefore to determine the distribution of different enamel prism packing patterns at different depths in the enamel in an extensive survey of the mature tissue in hominoids. The purpose of this is firstly; to explain the discrepancy between the results of Gantt et al (1977; Gantt, 1979; 1981) and those of Vrba and Grine (1978a; 1978b) and Boyde and Martin (1982; 1983). Secondly, to resolve whether enamel prism packing patterns have any taxonomic utility within the Hominoidea, and therefore whether thay can contribute to the resolution of the phylogenetic affinities of the later Miocene hominoids. Thirdly, to examine the cell biological evidence concerning the distribution of the different enamel prism packing patterns and concerning the way by which the observed thickness of enamel has been formed.

II. METHODS

The following preparative methods for mature enamel have been used in the present study (coding letters correspond with those used by Boyde and Martin (1982)):

H. Etching large polished facets, depth not defined, on extracted teeth

Samples were prepared by the commonly used technique of polishing a flat facet on a lateral tooth surface which was then etched with 0.5% H_3PO_4. Gantt (1979; 1980; 1981) and Gantt and Cring (1981) have also used this technique, Shellis and Poole (1977) have used this technique with a different etchant. The sample was air dried and a conductive (gold, gold-paladium) coating applied before being directly examined in the scanning electron microscope (SEM). Since fossil specimens are valuable, if not irreplaceable, the aim is to produce a small facet. This necessarily means that the enamel sampled is relatively close to the tooth surface. To sample deep enamel would require the production of large facets which would destroy a large portion of the external tooth morphology.

J. Replicas of etched polished facets of teeth in situ in museum specimens

Method H has the disadvantage that the teeth must be extracted, or be isolated or the specimen small in size in order that it may fit the specimen chamber of the SEM. This can be avoided by the use of

replicas. Small facets were polished on the buccal surfaces of intact teeth in jaws. Surrounding areas were protected with a paraffin wax film (Parafilm sealing tissue, Gallenkamp, London). The etchant (0.5% H_3PO_4) was applied and removed with a bacteriological pipette. After washing and air drying, a silicone rubber impression was taken of the etched surface and cast in araldite according to the technique described by Barnes (1978). A conductive coating was then applied to the replica prior to examination in the SEM.

K. Etching limited areas at known depths in extracted teeth

A single cylindrical groove was cut in the lateral surface of the tooth with the side of a 1mm diameter plane tungsten carbide cylindrical (fissure) bur, to a maximum depth of about 250 μm. The surrounding enamel surface was protected with nail varnish or a viscous solution of polymethyl methacrylate in chloroform to prevent etching. The groove was then etched with 0.5% H_3PO_4. This method offers some advantages over methods H and J (above) as it samples deep enamel but it samples it at a single depth. By replicating such a small, depth defined, groove in the surface of a tooth of a large specimen, the deep enamel prism pattern can be studied with very little damage to the specimen and the tooth does not need to be removed from the specimen, or be placed in the SEM.

L. Etching limited areas at a series of measurable depths

In pilot experiments designed to produce the maximum amount of

information from a tooth (given that a certain amount of tissue has to be destroyed in preparing a sample for enamel microstructure studies) I etched the enamel in the bottom of grooves cut with the diamond slicing wheel which I used to cut sections for enamel thickness measurements. The tooth surface was covered with nail varnish prior to cutting the 350 μm wide groove and samples were then etched with H_3PO_4 (0.5% - 2%) typically for 30 seconds. A special specimen stub was constructed such that the sample could be relocated precisely on both cutting machine and in the SEM. In this way a given cut could be extended incrementally and the etched enamel prism packing pattern investigation at a series of (measured) depths through the enamel.

This method has the great advantage, over all previous ones, that the enamel prism pattern can be observed at a variety of depths in a single plane in one tooth. The depths at which the pattern corresponding with the pattern observed in developing surface preparations appears (Boyde and Martin, 1982, 1983) could be measured so that comparisons can be made between homologous areas of enamel in different species. This method has the advantage that it can be used to study the enamel up to a depth of several hundred microns, far deeper than can be sampled by polishing facets, without damaging large areas of the tooth surface. The groove samples enamel at a continuous range of depths from shallow enamel at the cuspal and cervical ends of the groove to the deepest enamel at the centre of the groove.

An incrementally extended series of grooves provides evidence relating to enamel structure at locations whose relative depth is

known. I found it convenient to make replicas (see Method J above) of the etched groove at each sequential step prior to continuing the cut. This avoids the necessity of precisely relocating the specimen on the slicing wheel apparatus for sequential cuts. In addition, it provides a permanent record of the enamel prism pattern at a sequence of depths and the depth of each groove can be directly measured from the silicone rubber (negative) impression. The actual depth of a groove cut with the diamond slicing wheel is difficult to control with precision and small increments are impossible to achieve. The documentation of changes in enamel prism packing pattern at small and precisely measured increments requires the use of a tandem scanning reflected light microscrope. With this instrument it is possible to observe enamel structure at depths up to at least 200 μm non-destructively (Boyde, personal communication). As this equipment will be available to me later this year further destructive research was considered unjustified. The longitudinal sections cut for enamel thickness measurements have, instead, been exploited to provide microstructural data at all depths into the enamel, and to provide additional developmental information which cannot be directly obtained by any other method (see Method N).

N. Etched longitudinal sections

Potentially valuable information can be obtained by the light microscopic (LM) study of conventional ground sections (Kawai, 1955; Shellis and Poole, 1977). In the present work, I have tried to exploit one cut face, attempting, using SEM, to obtain as much

information as possible from the single cut which was made to expose the enamel for thickness measurements (examples of these faces are illustrated in Figure 4.11 - 4.26). The longitudinal sections were etched with H_3PO_4 (0.5% - 2%) after protecting the tooth crown surface with nail varnish to prevent etching of areas other than those under study. SEM study of etched longitudinal sections was used to determine the extent to which prism decussation occured. It can also be used to examine the relative compression of the incremental lines in the surface zone, the distance between the cross-striations of the prisms (the presumed daily incremental lines), and the widths of the diazones (prisms cut transversly) and of the parazones (prisms cut longitudinally). The cross striation repeat interval probably represents 24 hours of enamel development and may be used to determine the rate of enamel formation.

P. Plastic casts of hypoplastic tooth surfaces

It is not possible at present to extract useful information from developing tooth crowns which have been subject to drying as drying completely destroys the delicate young enamel structure (Boyde and Martin, 1982; 1983). This problem would be compounded by post mortem autolytic changes and bacterial decomposition so that there is no hope of observing the developing enamel surface morphology in fossilised tooth germs. However, the developing enamel surface morphology is preserved in the completed enamel surface of the mature tooth in the base of hypoplastic grooves in modern specimens (Boyde, 1970). In enamel hypoplasia the young enamel is preserved by mineralization from

within the tissue, and this may offer the possibility to observe the structure of the developing enamel surface in extinct species.

In order to investigate whether the surface of sub-fossil and fossil samples could be utilised to study the essential features of enamel development, I prepared resin casts of silicone rubber impressions of hypoplastic areas of teeth from two prehistoric samples, one from 400 B.P. archaeological human material and another from circa 14×10^6 B.P. fossil hominoid material from Pasalar, Turkey. These were all erupted functional teeth showing signs of occlusal wear and approximal contact wear facets. I was unable to identify ameloblastic pits on this material. However, A.D. Beynon (personal communication) has successfully replicated the Tomes' process pits in the grooves of perikymata in Paranthropus boisei. Should the opportunity present itself to study unerupted or partially erupted fossil primate teeth, these should be prepared with this possibility in mind and the fossilization matrix removed with extreme care.

III. RESULTS

The results for the enamel microstructure studies are presented under three headings: firstly prism cross sectional patterns in the sub-surface zone of the enamel at unspecified depth (methods H and J); secondly enamel prism patterns at a sequence of depths reaching the deeper (mid thickness) regions of the enamel (methods K and L); and thirdly aspects of enamel microstructure as revealed in etched longitudinal sections (method N). The enamel prism packing pattern varieties are described according to the definitions of Boyde (1964), and these are illustrated in Figure 5.1.

1. Prism cross sections at unspecified depth. Figure 5.2.

A small number of teeth were prepared by the method described by Gantt (1979). The results from these studies were inconsistent and are of limited interest for taxonomic purposes. The methods described as H and J above are designed such that only small facets are polished. This necessarily means that the enamel prism cross sectional patterns are sampled fairly close to the surface of the enamel. The results from these studies of shallow enamel prism packing patterns are, however, of use for the interpretation of the development of the outer portion of the enamel thickness.

Gorilla gorilla: Six molar teeth were examined and in most cases the enamel prism packing pattern was that described as Pattern 1 (Figure 5.2b). In one case a very large facet was accidentally prepared!, this cut into the deep enamel and revealed a Pattern 3 arrangement of

the prisms (Figure 5.2d).

Pan troglodytes: Six molar teeth were examined and the enamel prism packing pattern was Pattern 1 (Figure 5.2a).

Homo sapiens: Six molar teeth were examined, the prism packing pattern was almost invariably Pattern 3 (Figure 5.2c). Some areas of Pattern 1 enamel were encountered at the periphery of facets which is where the shallowest enamel is being sampled.

Ponyo pygmaeus: Six molar teeth were examined. The enamel prism packing pattern was usually Pattern 1 (Figure 5.2e). In the case of some of the largest facets, which sample deeper enamel at their centre, zones of Pattern 3 enamel were found in the centre (Figure 5.2f). In all of these cases the Pattern 3 area was surrounded by Pattern 1 enamel in the shallower enamel being sampled.

A few specimens of fossil teeth from the Siwaliks and from Pasalar were examined. Hominoid teeth from both of these localities usually revealed Pattern 3 enamel (Figure 5.2g and h). If the surface of the tooth was very lightly polished, so that no facet was visible, then Pattern 1 enamel was occasionally revealed.

These results are generally in accord with those reported by Gantt et al (1977; Gantt, 1979) although Gantt did not report Pattern 3 enamel in Gorilla or Pongo. It is clear that in Pongo, Homo, Gorilla and Sivapithecus the depth at which the enamel prism

packing pattern is sampled affects the pattern type which is observed. The taxonomic value of results using polished facets is therefore minimal and methods in which deeper enamel could be sampled, without undue tissue destruction (with very extensive facets), were therefore applied. It should be borne in mind that there is a layer of Pattern 1 enamel adjacent to the enamel-dentine junction in man, and in many mammals (Boyde, 1964). This layer is usually about 30 - 50 μm thick. References to deep enamel refer to the enamel deep to the surface layer but beyond the Pattern 1 layer adjacent to the enamel-dentine junction.

Figure 5.2: Enamel prism packing cross sections revealed in etched polished facets of undefined depth sampling the shallow enamel.

a) Facet polished on the mesio-buccal aspect of the paracone of a Pan troglodytes M^2 (Pa 2, Appendix A), etched with 0.5% H_3PO_4 for 60 seconds, cervix towards bottom. Field width = 100 µm.

b) Facet polished on the mesio-buccal aspect of the paracone of a Gorilla gorilla M^3 (Go 3, Appendix A), etched with 0.5% H_3PO_4 for 60 seconds, cervix towards bottom. Field width - 45 µm.

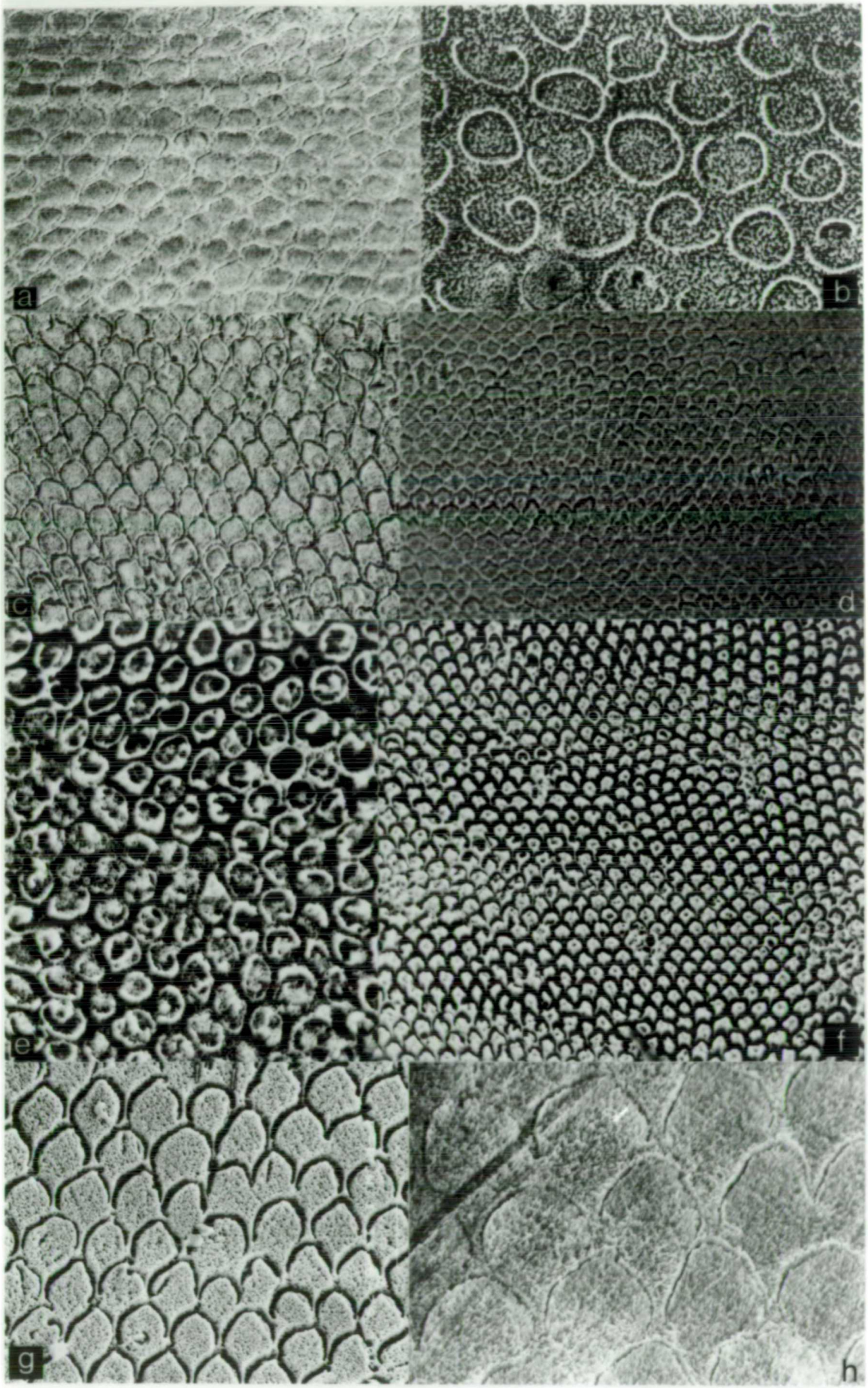
c) Facet polished on the buccal aspect of an upper molar of Homo sapiens, etched with 0.5% H_3PO_4 for 60 seconds, cervix to bottom. Field width = 75 µm.

d) Facet polished on the mesio-lingual aspect of the metaconid of a Gorilla gorilla M_3 (Go 9, Appendix A), etched with 0.5% H_3PO_4 for 120 seconds, cervix towards bottom. Field width = 191 µm.

e) and f) Facet polished on the mesio-buccal aspect of the metaconid of a Pongo pygmaeus M_1 (Po 19, Appendix A), etched with 2% H_3PO_4 for 60 seconds, cervix towards bottom. Figure 5.2e shows a Pattern 1 arrangement of the prisms which was found all over the facet except in the area shown in Figure 5.2f which is a zone of Pattern 3 enamel in the centre of the facet. This means that Pongo has Pattern 3 in the deeper enamel and Pattern 1 near the tooth surface. Field widths, e) = 77 µm, f) = 193 µm.

g) Pattern 3 enamel revealed in a facet polished on a molar of S.darwini from Pasalar, etched with 0.5% H_3PO_4 for 60 seconds, cervix towards bottom. Field width = 55 µm.

h) Pattern 3 enamel revealed in a facet polished on YPM-5018 from the Siwaliks, etched with 0.5% H_3PO_4 for 60 seconds, cervix towards bottom. Field width = 28 µm.


a
b
c
d
e
f
g
h

2. Enamel prism patterns in the deeper enamel (methods K and L) (Figure 5.3)

The use of a diamond saw cut groove permits the observation of enamel prism packing patterns at a series of depths when the cut is extended incrementally. The depth of the groove at any point could be measured by stereometry, but this was not done in the present work as I am unable to form three dimensional models from stereo photographs. For the purposes of the present work the exact depth at which changes in enamel prism packing patterns occur will be determined from longitudinal sections. The purpose of the etched grooves was to sample the deeper layers of enamel and to contrast the enamel prism packing patterns found there with those found near the tooth surface revealed by polished facets or by shallow diamond slicing wheel grooves. This method did not sample the thin layer of Pattern 1 enamel found adjacent to the enamel-dentine junction.

Pan troglodytes: In all cases the initial shallow groove revealed entirely Pattern 1 prisms. When these grooves were extended incrementally to the point where the groove was in the region of 0.3 mm deep Pattern 3 enamel was revealed (Figure 5.3.a).

Gorilla gorilla: As was suggested by the presence of Pattern 3 enamel in the deepest enamel sampled by a very large polished facet, Gorilla shows the same distribution pattern as Pan. The surface enamel is entirely Pattern 1 and is of relatively great thickness. When the groove samples deep enamel then Pattern 3 prisms are found.

Homo sapiens: Even the shallowest groove cut revealed Pattern 3 enamel, although zones of Pattern 1 enamel may be found at the periphery of the groove. This confirms the findings from polished facets, that Homo has a relatively thin outer layer of Pattern 1 enamel, below which is Pattern 3 enamel.

Pongo pygmaeus: Shallow grooves reveal entirely Pattern 1 enamel. Slightly deeper grooves reveal Pattern 3 enamel (Figure 5.3b). The outer layer of Pattern 1 enamel is thicker than that in Homo, but is much less thick than in Pan and Gorilla.

Hylobates: Shallow grooves revealed Pattern 3 enamel (Figure 5.3c and d). Restricted zones of Pattern 1 enamel were encountered at the cuspal and cervical ends of the grooves which sample the shallowest enamel. This situation is most similar to that seen in Homo.

Sivapithecus: A number of specimens sampling the four species from Pasalar and the Siwaliks, which were used for enamel thickness measurements (Table 4.3), provided evidence regarding enamel structure in these species. The results for all specimens are the same. Even shallow grooves which just mark the tooth surface reveal predominantly Pattern 3 enamel, although zones of Pattern 1 enamel may be visible at the cuspal and the cervical end of the groove. A shallow groove in a S.sivalensis molar is shown in Figure 5.3e and the prism Pattern in Figure 5.3f. In specimens from Pasalar and from the Siwaliks Pattern 3 areas are often encountered immediately subsurface (Figure 5.2g and

h), within a few microns of the tooth surface. This distribution of enamel prism packing patterns is most like that found in Homo and in Hylobates.

These results which provide evidence regarding enamel prism packing patterns in deep enamel as well as at a series of relative depths are consistent with those for the developing enamel surface. All hominoids show a predominance of Pattern 3 enamel in the developing enamel surface preparations which sample the deep enamel (Boyde and Martin, 1982, 1983). The results described above for mature enamel sampled in the deep layers explains the discrepancy between the results of Gantt et al (1977; Gantt, 1979) and those for developing enamel (Boyde and Martin, 1982, 1983). The enamel structure described by Gantt (1977, 1979) for the great apes was that which is found in the subsurface zone of the enamel.

The deep enamel in all extant hominoids, and in the Eurasian Sivapithecus, is Pattern 3, and this is true for both mature and developing enamel. Homo, Sivapithecus and Hylobates have Pattern 3 enamel extending close to the tooth surface. Pongo has a relatively thick zone of Pattern 1 enamel below the tooth surface overlying the Pattern 3 deep enamel. Pan and Gorilla have a very thick layer of Pattern 1 enamel overlying the deep Pattern 3 enamel. This means that methods for examining the predominant structure of the mature enamel must be able to sample the enamel at a depth measured in hundreds of microns. This rules out the use of polished facets as these would have to be very large if they were to expose this depth of enamel at the centre of the facet.

Figure 5.3: Enamel prism packing patterns revealed in the etched base of diamond slicing wheel grooves.

a) Pan. Pattern 3 enamel exposed in a deep groove on the buccal side of the metacone of M^1, etched with 2% H_3PO_4 for 60 seconds after treatment with 5% NaOCl for 2 hours, cervix towards bottom. Field width = 360 µm.

b) Pongo. Pattern 3 enamel exposed in a groove on the lingual side of the metaconid of M_1 (Po 19, Appendix A), etched with 1% H_3PO_4 for 60 seconds, cervix towards bottom. Field width = 71 µm.

c) Hylobates. Pattern 3 enamel in a very shallow groove on the side of an M_1, etched with 2% H_3PO_4 for 60 seconds, cervix towards bottom. Field width = 119 µm.

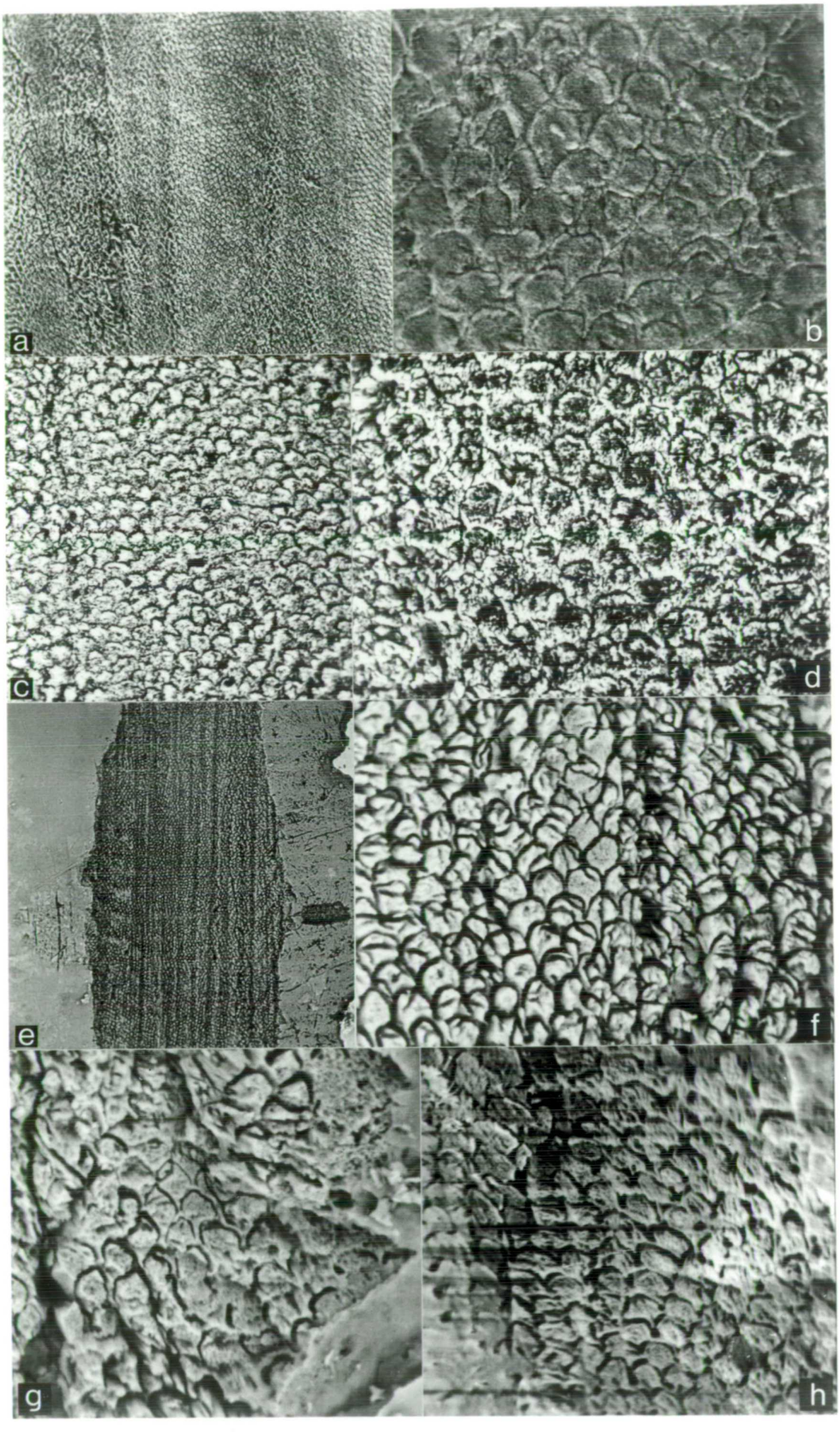
d) Hylobates. Close up of Pattern 3 enamel in groove shown in Figure 5.3c. Field width = 71 µm.

e) S.sivalensis. Groove on the lingual side of the metacone of M^1 (M 13366), etched with 1% H_3PO_4 for 150 seconds, cervix towards bottom. Field width = 640 µm.

f) S.sivalensis. Pattern 3 enamel in middle of groove shown in Figure 5.3e. Field width = 88 µm.

g) S.sivalensis. Cervical end of groove shown in Figure 5.3e. Field width = 73 µm. The tooth surface can be seen at the right side of the picture. This shows that Pattern 3 enamel is found very close, within about 10 µm, to the tooth surface.

h) S.darwini. Groove cut on the lingual side of the metaconid of M_3 (BP 4), etched with 1% H_3PO_4 for 120 seconds, cervix towards bottom. Field width = 68 µm. The tooth surface can be seen at top right. As in S.sivalensis, Pattern 3 enamel extends right up to the tooth surface.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3. Enamel microstructure revealed in polished and etched longitudinal sections

Polished and etched longitudinal sections may be used to provide evidence regarding aspects of enamel microstructure which are not readily studied by methods providing cross sections of enamel prisms (above). In particular they provide evidence as to the extent of prism decussation, from the Hunter-Schreger bands (Figures 5.4 - 5.10). When specimens are correctly prepared i is possible to observe incremental features of enamel growth: incremental lines (Figures 5.5c, 5.7d, 5.8b), prism cross striations (Figure 5.4 - 5.10) and perikymata (Figure 5.8a). In addition, alternate Hunter-Schreger bands reveal cross sections of the enamel prisms (Figure 5.4 - 5.10), this allows the observation of enamel prism packing patterns in the deep enamel. When Hunter-Schreger bands extend to close to the tooth surface then prism packing patterns in shallow enamel can be observed. Many methods for examining prism cross section (facets and grooves, above) do not cut into the decussating zones. This is evident from the fact that only cross sections are revealed in these preparations, not cross sections as well as length sections as are seen in longitudinal section preparations.

Homo sapiens: Longitudinal sections show that Huner-Schreger bands extend from the enamel-dentine junction to within 200 to 300 microns of the tooth surface (Figure 5.4a). Prism decussation, as evidenced by Hunter-Schreger ba ,w s found in all of the enamel except that vertically above the tips of the dentine horns (Figure 5.4d). There

is also a thin layer of enamel adjacent to the enamel-dentine junction which is non-decussating.

The enamel over the tip of the dentine horn has formed very slowly and has a cross striation repeat interval of 1.3 - 1.4 μm (Figure 5.4b). The rest of the occlusal basin enamel has Hunter-Schreger bands but these tend to have wider parazones (zones of parallel prisms) than is the case for the lateral enamel (Figure 5.4e). In these areas of occlusal enamel the cross striation repeat intervals were 5.5. - 6.1 μm. In the deep lateral enamel, where decussation permits the recognition of Pattern 3 prisms, the cross striation repeat interval is in the region of 6 - 7 μm (Figure 5.4c).

The enamel adjacent to the enamel-dentine junction and over the cusp tips is usually Pattern 1 in humans, and indeed in almost all mammals (Boyde, 1964). The enamel closest to the enamel-dentine junction is the first enamel formed during the life of an ameloblast. This enamel is formed slowly with cross striations, presumed daily incremental lines, between 1.3 and 1.4 μm apart. In human teeth, enamel close to the enamel-dentine junction, over the cusp tips, and close to the tooth surface is non-decussating and has formed slowly with cross striation repeat intervals of less than 1.5 μm. In these areas Pattern 1 prisms predominate. In areas with Hunter-Schreger bands the prisms are Pattern 3 and cross striation repeat intervals are 5 - 7 μm.

Figure 5.4: Etched, polished longitudinal sections through the mesial cusps of Homo sapiens molars.

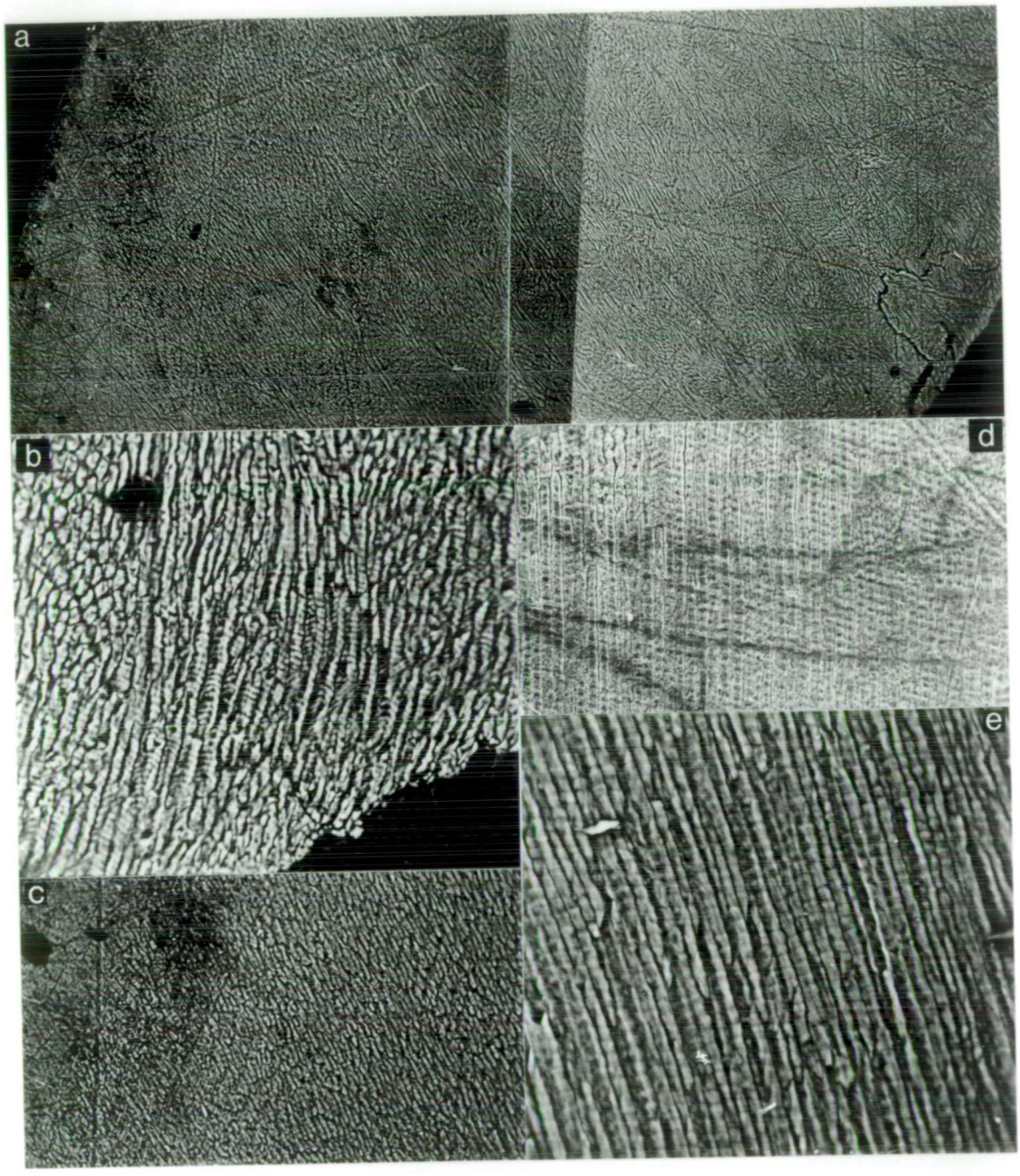
a) Montage across the buccal enamel of M^2 (Ho 14, Appendix A) at the level of enamel thickness measurement m (Figure 4.2), etched with 0.5% H_3PO_4 for 30 seconds. Cuspal towards top, enamel-dentine junction to right, tooth surface to left. Field width = 2.0 mm.

b) Longitudinal section through the mesial cusps of M^2 (Ho 14, Appendix A), polished to a 1 µm finish, etched with 0.5% H_3PO_4 for 30 seconds. This picture shows the enamel at the enamel-dentine junction of the buccal cusp tip. Cuspal towards top, tip of buccal dentine horn to bottom right. The banding pattern on the obliquely sectioned prisms is the prism cross striations, the daily incremental lines, these are spaced at 1.4 µm intervals in this region. Field width = 210 µm.

c) Prism cross striations near the lateral tooth surface, in shallow, Pattern 3, enamel in the section shown in Figure 5.4a. Tooth surface is at top left, cervical towards bottom. Field width = 516 µm.

d) Parallel prisms in cuspal enamel near the tooth surface, field width = 300 µm.

e) A parazone, showing obliquely sectioned prisms in occlusal fovea enamel just lingual to the midline of M^2. This portion of occlusal enamel has Hunter-Schreger bands. The cross striation repeat interval is 6.10 µm. Cuspal to top. Field width = 204 µm.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Pan troglodytes: The Hunter-Schreger bands in chimpanzee enamel are distributed in the same way as those in human enamel. However, they extend only 60% of the way from the enamel-dentine junction high up the tooth side where the enamel is thickest (Figure 5.5a), although more cervically they extend across a greater proportion of the enamel thickness (Figure 5.5b, c and d). In both areas the Hunter-Schreger bands cover the same absolute distance, about 500 μm from the enamel-dentine junction. In the low lateral enamel the prism cross section is Pattern 3 close to the tooth surface and there is no compression of incremental lines in the surface zone (Figure 5.5c). In these areas of decussating Pattern 3 enamel cross striations are visible on the more obliquely sectioned prisms and are spaced at 6 - 7 μm intervals (Figure 5.5d and e). This is similar to the rate at which human Pattern 3 enamel forms. Similarly the deep enamel high up the side of the teeth is Pattern 3 in the areas with Hunter-Schreger bands.

Figure 5.5: Etched, polished longitudinal sections through the mesial cusps of Pan troglodytes molars.

a) Showing the extent of Hunter-Schreger bands, enamel-dentine junction is to bottom left, tooth surface to top right. Field width = 904 µm.

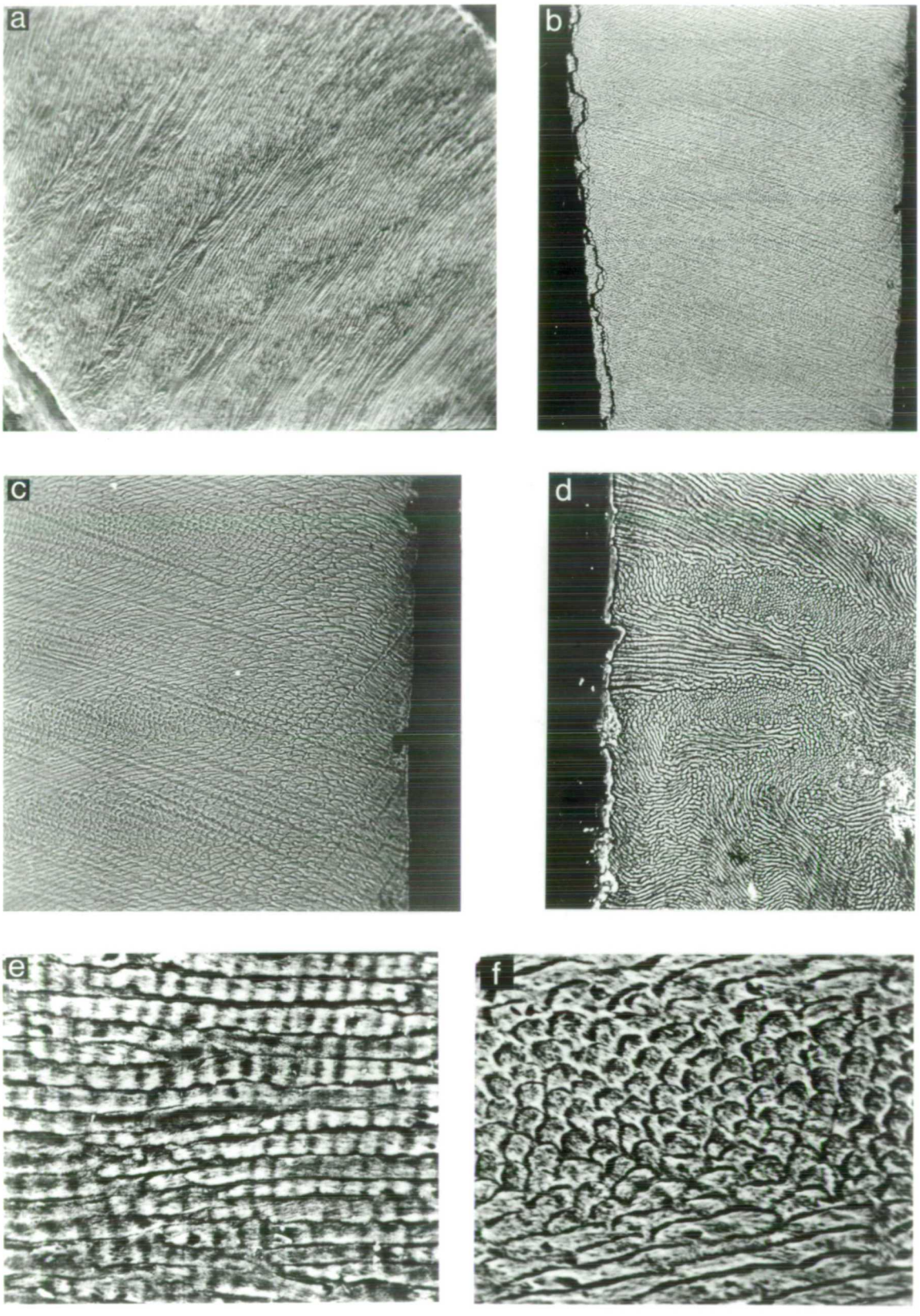
b) Low lateral enamel showing Hunter-Schreger bands extending across the whole enamel thickness, cuspal to top, enamel-dentine junction to left. Incremental features can be seen near the tooth surface to right, there is no compression of the incremental lines, in other words enamel development is rapid across the whole thickness of the low lateral enamel. Field width = 829 µm.

c) Close up of Figure 5.5b, showing Pattern 3 enamel, and Hunter-Schreger bands, extending close to the tooth surface in the low lateral enamel, cuspal to top, tooth surface to right. Field width = 488 µm.

d) Low lateral enamel, cuspal to top, tooth surface to left. Some cross striations are visible near the top of the picture, these are spaced at 6 µm intervals and show that low lateral enamel develops at the fast rate for its entire thickness. Field width = 528 µm.

e) Cross striations in low lateral enamel, cuspal to top. Increment spacing is 6.44 µm. Field width = 118 µm.

f) Pattern 3 enamel in the deep layers of enamel on the lingual cusp, cuspal to top, tooth surface to right. Field width = 95 µm.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Gorilla gorilla: The Hunter-Schreger bands are distributed in the same way as in Homo and in Pan. As in Pan Hunter-Schreger bands were found to extend only about 600 μm from the enamel-dentine junction. This means that they cover about 60% of the enamel thickness high up the side of the teeth (Figure 5.6a and b), but extend across most of the thickness where enamel is thinner, i.e. cervically, (Figure 5.6c). As in humans Hunter-Schreger bands are found in the occlusal fovea enamel but not over the cusp tips (Figure 5.6d). In all areas where Hunter-Schreger bands were found the enamel prism packing was Pattern 3 (Figure 5.6e). Cross striations were rarely visible in Gorilla specimens, where they were encountered in Pattern 3 areas they were spaced at 5 - 6 μm intervals.

Figure 5.6: Etched, polished longitudinal sections through the mesial cusps of Gorilla gorilla molars. Back scattered electron images, scanning electron microscopy.

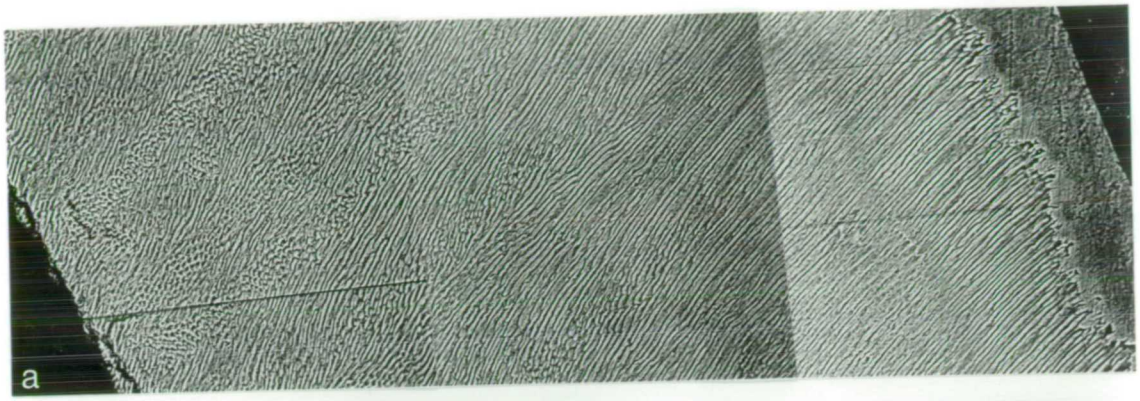
a) Montage showing the lateral enamel on the lingual cusp of M^1 (G 13, Appendix A), etched with 0.5% H_3PO_4 for 45 seconds. The enamel-dentine junction is to the left, tooth surface to right, cuspal to top. Prisms decussate for about 55% of the enamel thickness and then there is a wide zone of parallel prisms. Field width = 1045 µm.

b) Mid-lateral enamel on the lingual cusp of M^1, enamel-dentine junction to left, tooth surface to right, cuspal to top. The diazones, with transversly sectioned prisms, are narrow. Field width = 2.5 mm.

c) Lingual cingulum of M^1, enamel-dentine junction to left, tooth surface to right, cuspal to top. Field width = 1.64 mm. The cingulum is formed in the dentine, not by local differences in enamel thickness as Butler (1956) suggested. As the enamel becomes thinner, cervically, the Hunter-Schreger bands extend across a relatively greater proportion of the enamel thickness.

d) Enamel microstructure over the tip of the dentine horn, the dentine horn is at the bottom, cuspal to top. Hunter-Schreger bands extend laterally and medially, with respect to the whole tooth, but the enamel vertically over the cusp tip has parallel prisms only. Field width = 1.0 mm.

e) Lateral enamel of the buccal cusp of M^1. This photograph shows obliquely sectioned Pattern 3 enamel at the lateral edge of the Hunter-Schreger band region, in the mid thickness enamel. Field width = 51 µm.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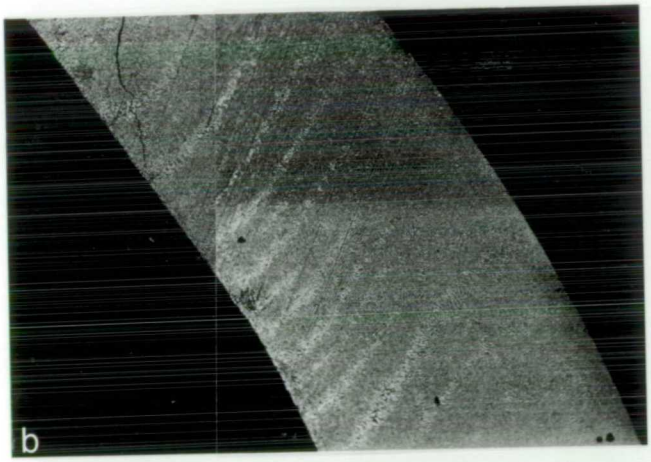
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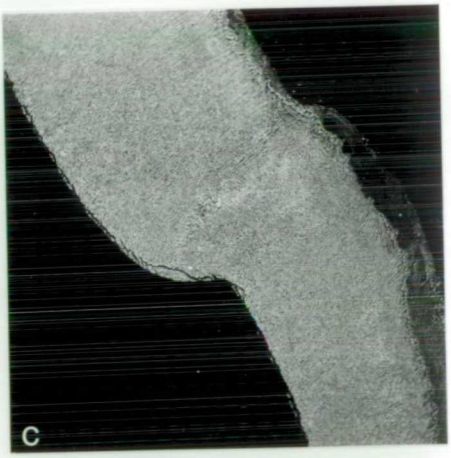
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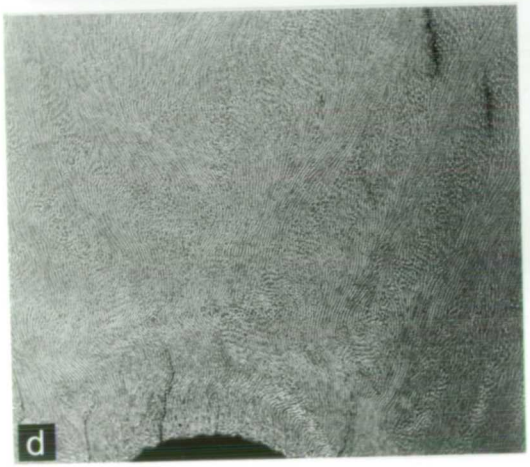
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Pongo pygmaeus: Hunter-Schreger bands are well marked and extended for 750 - 1000 μm (70 - 75%) from the enamel-dentine junction (Figure 5.7c). At the level of the base of the occlusal fovea enamel, where enamel thickness measurements (k) - (n) (Figure 4.2) were taken, there is an outer layer about 300 - 350 μm thick which does not show Hunter-Schreger bands (Figure 5.7a). More cervically, where the enamel is thinner, the Hunter-Schreger bands extend across the entire thickness of the enamel (Figure 5.7b).

The cross striation repeat interval varies within the non-decussating zone (Figure 5.7a). The outermost 40 - 50 μm has a cross striation repeat interval of about 1.8 μm. About 150 μm into the enamel the cross striation repeat interval is between 2.5 - 2.8 μm (Figure 5.7a). This means that orang-utan ameloblasts slow down gradually, and the rate of enamel formation is only very slow for the final 40 -50 μm. In some preparations the major incremental markings, called incremental lines (= brown striae of Retzius in light microscropy) were visible (Figure 5.7d). The prism cross striations are visible between the incremental lines. These are evenly spaced except at the outside of the tooth where the cross striations, and incremental lines, are compressed. This region where ameloblast secretion is slow is about 55 μm thick (Figure 5.7d).

The enamel prism cross section can only be determined from longitudinal sections in the Hunter-Schreger bands zone. The prism type is Pattern 3 right up to the lateral edge of the Hunter-Schreger band zone (Figure 5.7a).

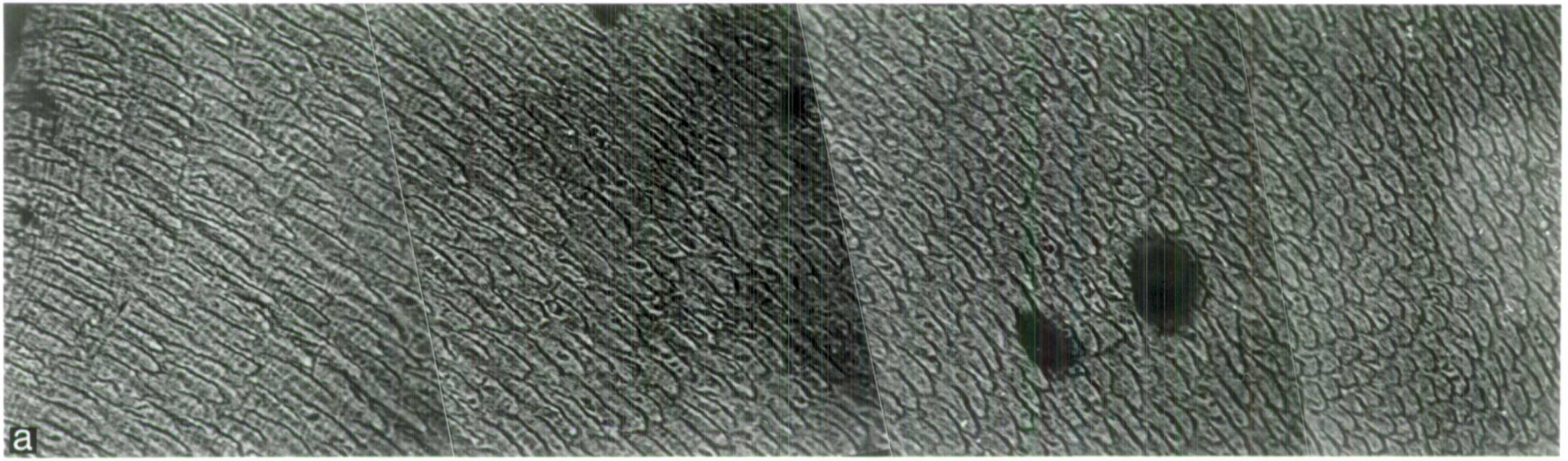
Figure 5.7: Etched, polished longitudinal sections through the mesial cusps of Pongo pygmaeus molars. Back scattered electron imaging by scanning electron microscopy.

a) Montage of the lateral enamel of the lingual cusp of M^2 (Po 5, Appendix A), etched with 1% H_3PO_4 for 45 seconds, tooth surface to left, cuspal to top. The montage extends from the tooth surface at left, to the deep enamel where diazones and parazones are well defined. The cross striation repeat interval is greatly reduced in the outermost 40 µm of the enamel thickness. Field width = 535 µm.

b) Low lingual enamel showing Hunter-Schreger bands extending across the full width of the enamel. Cuspal to top, enamel-dentine junction at right, tooth surface at left (M^1, Po 13, Appendix A). Field width = 688 µm.

c) Section treated with NaOCl for 3 hours, followed by 18 hours in EDTA pH 7.2, showing the cuspal enamel, with Hunter-Schreger bands extending across about 67% of the enamel thickness (measured radially), i.e. for about 1150 µm, the thickness without Hunter-Schreger bands is about 570 µm.

d) Lateral enamel, cuspal to top, tooth surface to right, showing incremental lines (brown striae of Retzius), and the cross striations in between them. There is a layer, about 53 µm thick, of enamel in which the cross striation repeat interval is reduced. Field width = 367 µm.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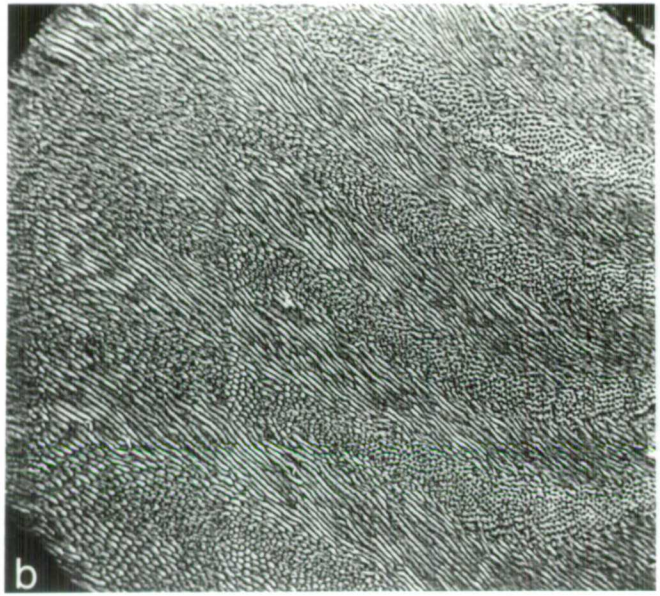
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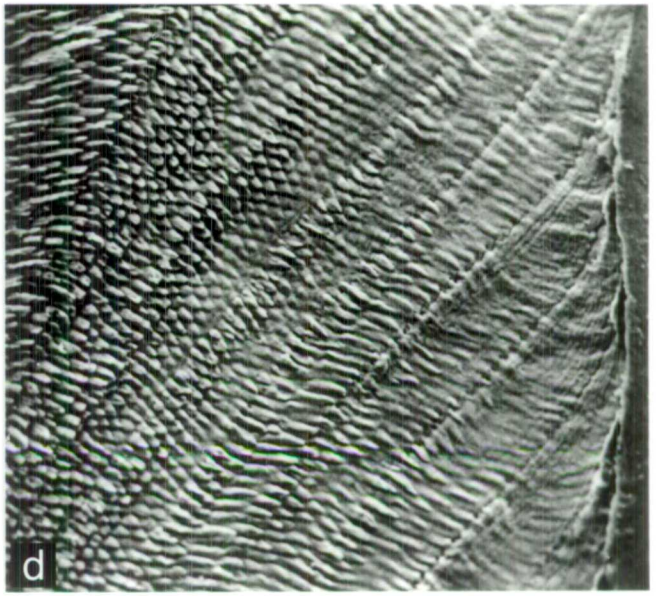
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Hylobates lar: Gibbon enamel shows less decussation than does that of man and the great apes. Hunter-Schreger bands are visible and extend across about half the thickness of the enamel (about 275 μm) from the enamel-dentine junction (Figure 5.8a). Diazones, where prisms are sectioned transversely, are narrow in the more cuspal lateral enamel, and no Hunter-Schreger bands are defined in the thinner, more cervical enamel (Figure 5.8b).

The deep enamel is Pattern 3 (Figure 5.8c) and obliquely sectioned prisms have a cross striation repeat interval of 4.5 - 5.5 μm. This cross striation repeat interval extends into the outer half of the enamel, where no Hunter-Schreger bands are defined. There is an outer layer of enamel on the mid-lateral crown in which cross striations are very close together with repeat intervals 1.7 - 1.8 μm (Figure 5.8d). Interestingly, there is a layer of transversely sectioned prisms immediately deep to the slowly formed outer 20 - 35 μm of enamel (Figure 5.8e and f) and these prisms are invariably of Pattern 3 cross section. The low lateral enamel has evenly spaced incremental lines and cross striations until just before the surface of the tooth is reach (Figure 5.8b). The correlation of incremental lines with perikymata is clearly visible in gibbon enamel (Figure 5.8a and b).

Figure 5.8: Etched polished longitudinal section through the mesial cusps of Hylobates M_3. Section polished to a 1 µm finish, etched with 0.5% H_3PO_4 for 30 seconds.

a) Montage across the lateral enamel of the buccal cusp at the level of enamel thickness measurement m (Figure 4.2). Hunter-Schreger bands are poorly defined with very narrow diazones (transversely sectioned prisms). Enamel-dentine junction to right, tooth surface to left, cuspal to top. Field width = 566 µm.

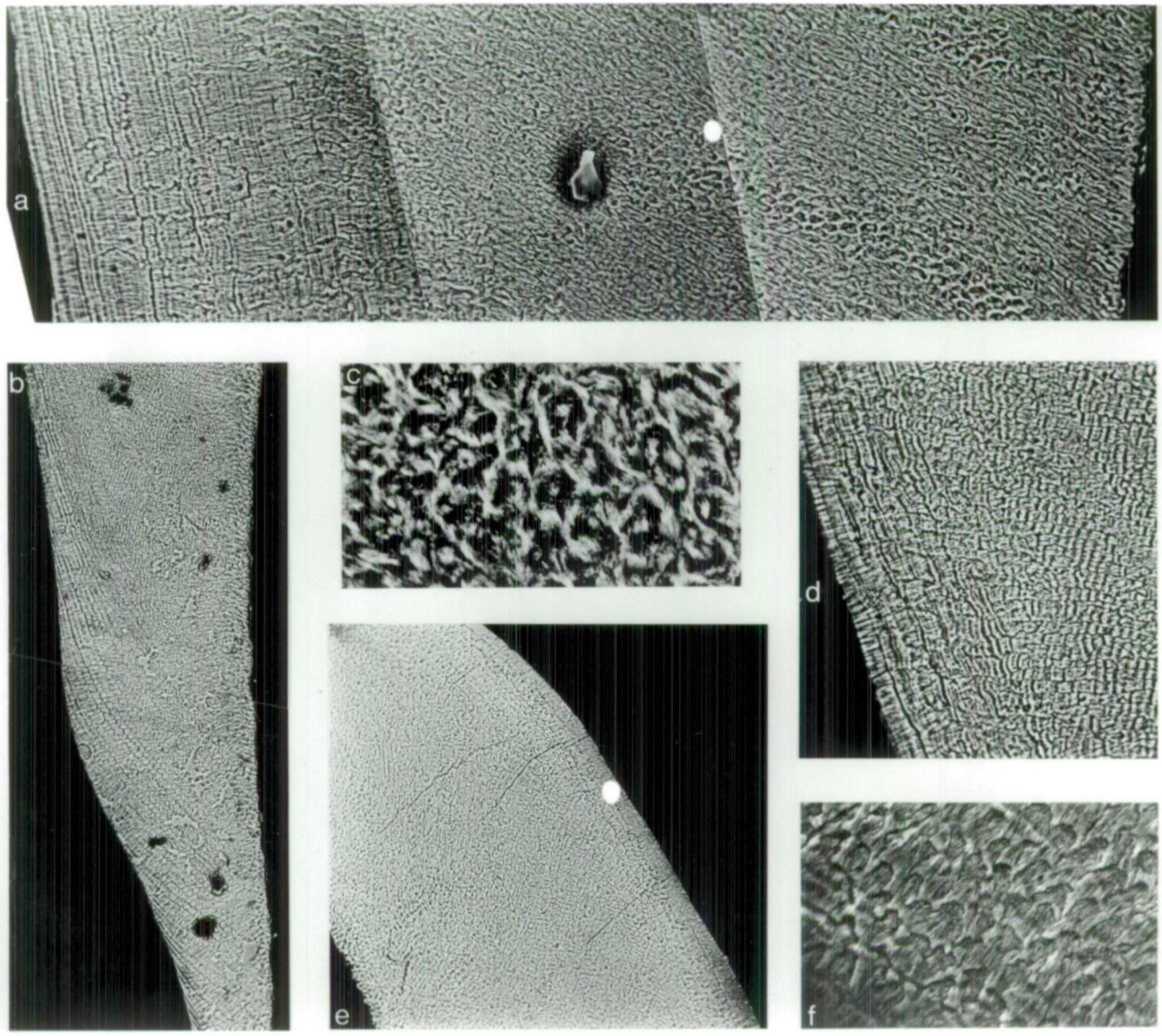
b) Enamel lower down on the buccal side of the tooth, cuspal to top, enamel-dentine junction to right, tooth surface to left. The figure shows that there is only a very narrow zone of enamel in which the cross striation repeat interval is reduced, about 12 µm thick. The deep enamel is all fast formed. Field width = 350 µm.

c) Pattern 3 prism cross section in deep enamel on the buccal side of the tooth. Field width = 50 µm.

d) Lateral enamel on the buccal side of the tooth, cuspal to top, tooth surface to left. The zone in which the cross striation repeat interval is reduced is 33 µm thick. Field width = 176 µm.

e) Lateral and cuspal enamel of the lingual cusp, cuspal to top, tooth surface to right, enamel-dentine junction at bottom left. The outer layer, in which cross striation repeat intervals are reduced, is 15 - 20 µm thick in this area where the maximum enamel thickness is developed. Field width = 550 µm.

f) Close up of the Pattern 3 enamel prisms in the layer immediately deep to the slowly formed surface layer (Figure 5.8e). Cuspal to right, field width = 90 µm.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Sivapithecus:

All four species of Sivapithecus (S.sivalensis, S.punjabicus, S.darwini, and S.alpani) have the same enamel structure as far as this study has been able to ascertain. They all show a high degree of prism decussation. Hunter- Schreger bands are clearly defined and extend for 85 - 100% of the enamel thickness (measured along the mean prism long axis, i.e. parallel to the Hunter-Schreger bands) even where the enamel is thickest (Figure 5.9a and b, 5.10a and b). In some specimens the Hunter-Schreger bands may not appear to extend across the full width of the enamel in low magnification photographs (Figure 5.9a). In these cases higher magnification photographs show that prism decussation continues into the outer layer of enamel but the degree of decussation (or angle of crossover) is less than in the deepest enamel so that bands are not so clearly defined (Figure 5.9b and d). In almost all specimens studied the actual thickness of the zone with paralled prisms was about 50 μm thick. In one area of a specimen of S.sivalensis a patch of Pattern 1 enamel was encountered near the tooth surface, extending into the enamel to a depth of about 150 μm (Figure 5.10c). However, adjacent areas on the same tooth show Pattern 3 enamel extending to within about 30 μm of the tooth surface (Figure 5.10b). The presence of this Pattern 1 zone may be significant but since it was of isolated extent in only one specimen its significance cannot be determined at present.

In all areas with decussating enamel the prisms are of Pattern 3 cross section (Figure 5.9e and f, 5.10b). This is true even at the

outside of the tooth where the prisms are very obliquely sectioned, so that they appear almost parallel (Figure 5.9d). The cross striation repeat interval in deep enamel is 5 - 6 μm (Figure 5.9b). The cross striation repeat interval in the outermost layer of parallel prisms is also 5 - 6 μm (Figure 5.9c and d). This is the same rate as is found in the deep enamel in all extant hominoid species. Except for the single patch of Pattern 1 enamel noted above there is no evidence of ameloblasts slowing down their secretion rate towards the end of their lives.

Figure 5.9: Etched, polished longitudinal sections through the mesial cusps of Sivapithecus molars from Pasalar, Turkey.

a) Montage of the lingual enamel of a S.alpani M_2 (BP 13), etched with 0.5% H_3PO_4 for 30 seconds, enamel-dentine junction to right. Hunter-Schreger bands extend across most of the enamel thickness, even where the thickness is at a maximum. Only the region above the tip of the dentine horn has no prism decussation. Field height - about 4.27 mm.

b) Montage across the lateral enamel of the lingual cusp of a S.alpani M_2 (BP 13), polished to a 1 μm finish for 180 seconds, etched with 1% H_3PO_4 for 120 seconds, enamel-dentine junction to right, tooth surface to left, cuspal to top. The montage is in the plane of enamel thickness measurement n (Figure 4.2). Although diazones and parazones are faint in the outer layer of enamel, prism decussation is clearly visible to within a short distance of the tooth surface. Obliquely sectioned Pattern 3 prisms are visible just deep to the tooth surface. Field width = 1132 μm.

c) Low lingual enamel of a S.darwini M_3 (BP 4), etched with 0.5% H_3PO_4 for 30 seconds, cuspal to top, tooth surface to left. Hunter-Schreger bands extend right up to the tooth surface. Field width = 408 μm.

d) S.alpani M_2 (BP 13). This shows the enamel just cuspal to enamel thickness measurement n (Figure 4.2) on the lateral aspect of the lingual cusp, cuspal to top, tooth surface to left. This is the region where the maximum thickness of enamel is observed, and the prism cross striations are clearly visible in the outermost enamel and their repeat interval is 5.7 μm. In other words, the outer enamel has formed quickly and there is no sign of a slowed down zone of enamel formation. In regions where the prisms are sectioned less obliquely, it is clear that the prism type with this cross striation repeat interval is Pattern 3. Field width = 213 μm.

e) S.alpani M_2 (BP 13). Mid-thickness lateral enamel on the buccal side of the tooth, Pattern 3 prism cross section. Field width = 31 μm.

f) S.alpani M_2 (BP 13). Mid-thickness occlusal fovea enamel, Pattern 3 cross section. Field width = 76 μm.

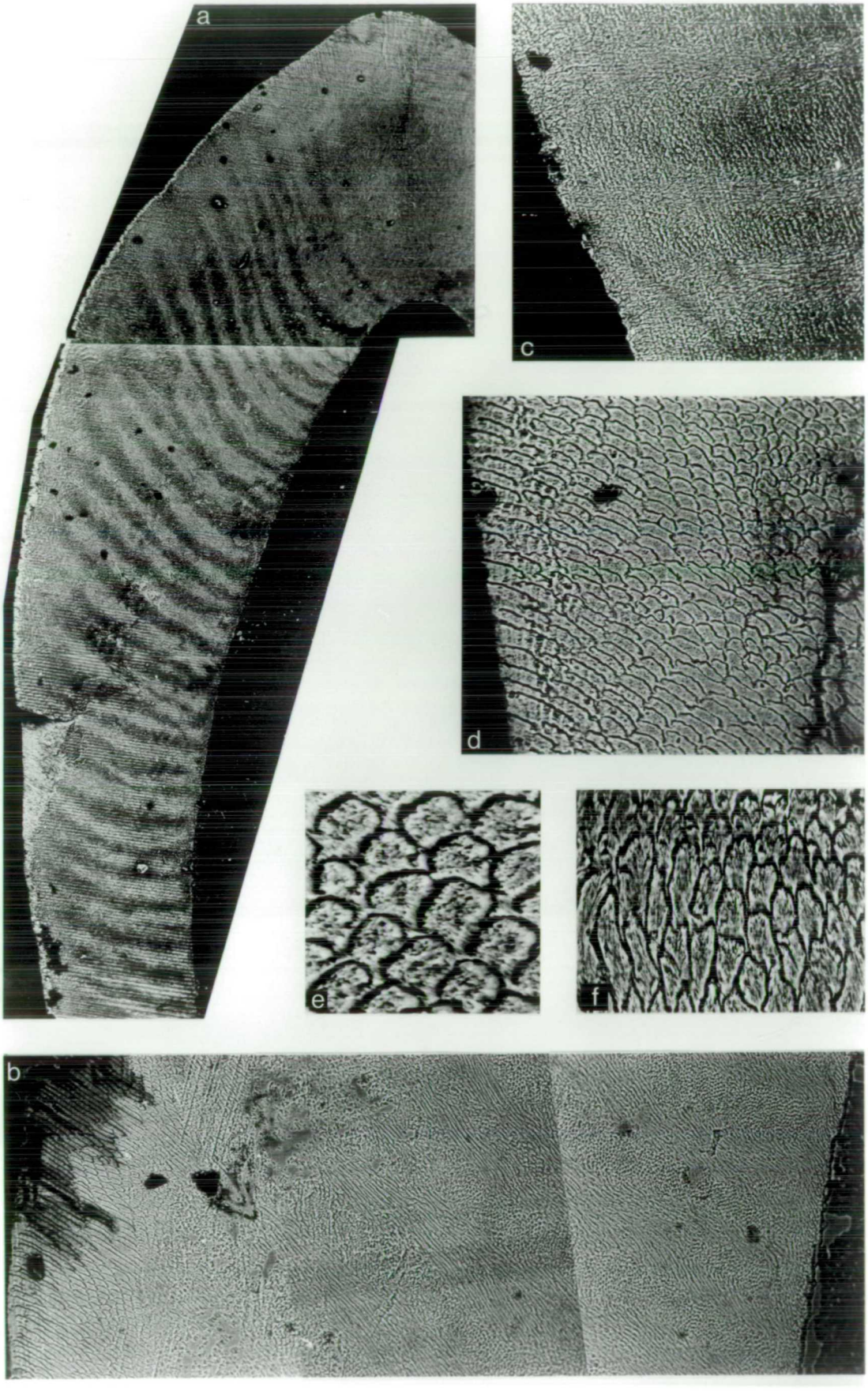
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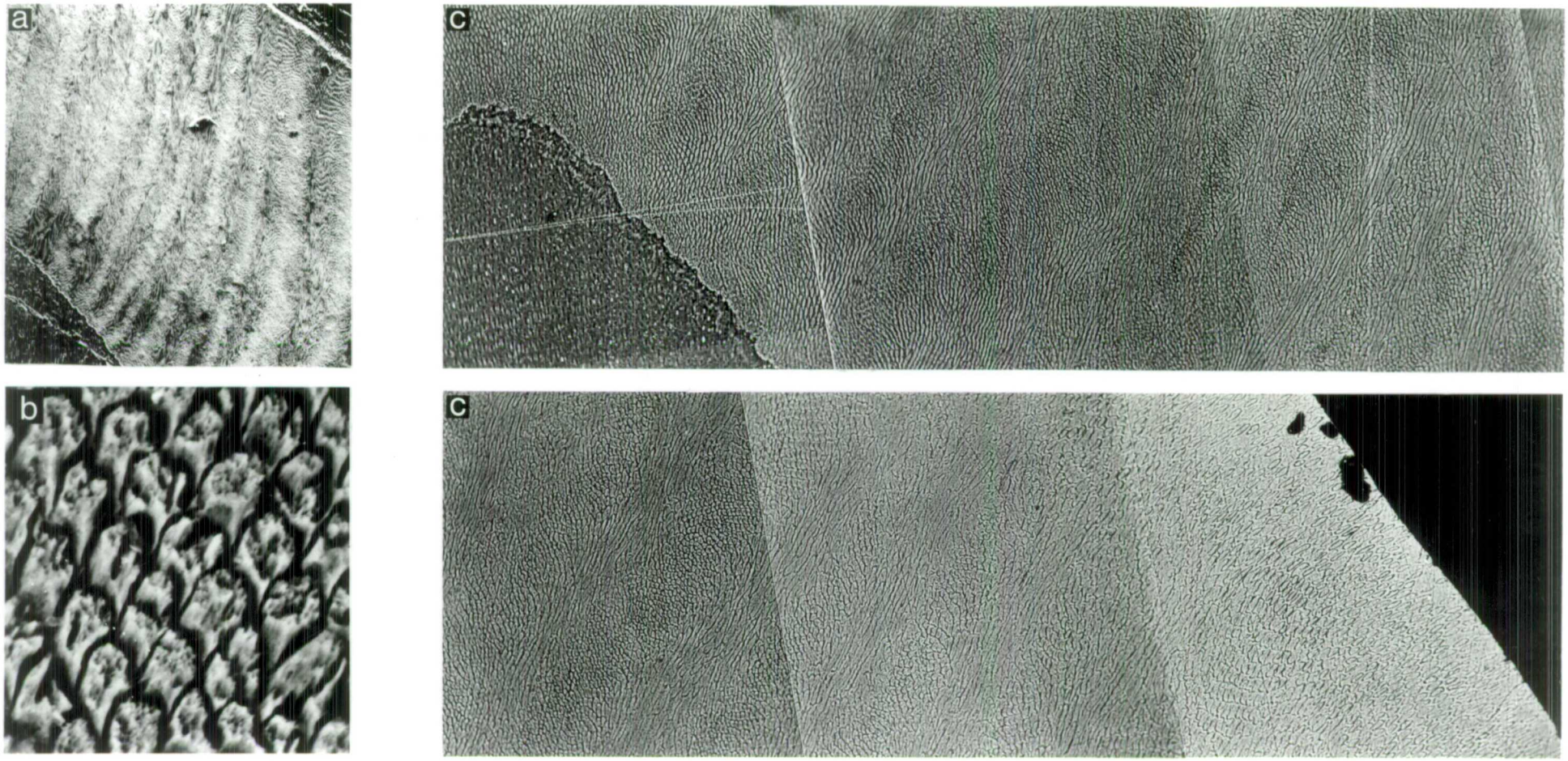
Figure 5.10: Etched, polished longitudinal sections through the mesial cusps of Sivapithecus molars from the Siwaliks.

a) Section through M_1 (AMNH 19565-B), cuspal to top, enamel-dentine junction at bottom left, tooth surface at top right. Hunter-Schreger bands are well developed and extend to the tooth surface even where the enamel thickness is at a maximum.

b) Sivapithecus sivalensis M^1 (M 13365) section polished to a 1 µm finish, etched with 0.5% H_3PO_4 for 30 seconds. Pattern 3 area immediately subsurface in buccal enamel, cuspal to left. Field width = 35 µm.

c) Sivapithecus sivalensis M^1 (M 13365), montage across the lateral aspect of the lingual cusp at the level of the maximum thickness of the enamel. The montage has been divided in two as it is too wide to be shown at a useful magnification otherwise. The right hand end of the upper part of the montage, which shows the tip of the dentine horn, joins the left hand end of the montage below it, which shows the tip of the tooth surface at the right, cuspal is towards the top. Hunter-Schreger bands extend most of the way to the tooth surface. In this particular area, there is an outer layer showing obliquely sectioned Pattern 1 enamel. As shown in Figure 5.10b, this is not the case for all regions of this specimen. This section confirms that the region of the enamel with Hunter-Schreger bands is Pattern 3, while the area without the Hunter-Schreger bands has Pattern 1 prisms. The total field width for both parts of the montage is 2.4 mm, each half of the montage has a field width of 1.2mm.


a
b
c
c

IV. THE RATE OF FORMATION OF HOMINOID ENAMEL

All of the hominoids examined show Pattern 3 enamel in the deep layers except for the thin layer of Pattern 1 enamel adjacent to the enamel-dentine junction. In Homo, Hylobates, and Sivapithecus Pattern 3 prisms extend to within 20 - 30 μm of the tooth surface even where the enamel is thickest. Pongo has an outer layer of Pattern 1 enamel in the areas sampled by facets and by grooving, which tend to be high up the lateral surface. Pan and Gorilla have a greater thickness of Pattern 1 enamel in these areas such that Pattern 3 prisms were only found when the facets or grooves cut very deeply into the enamel.

In all species the areas of enamel with Pattern 1 cross section have formed slowly, as evidenced by cross striation repeat intervals and incremental line spacing. In these regions cross striation repeat intervals are less than 2 μm. In all of the living hominoids Pattern 3 enamel is associated with cross striation repeat intervals of 5 - 7 μm. In other words Pattern 3 enamel is formed much more quickly than Pattern 1 enamel in hominoids. As the outer layers of enamel, as well as that adjacent to the enamel-dentine junction, are formed by the same ameloblasts as form the deep enamel it follows that in hominoids ameloblasts secrete enamel slowly for the first period of their life, when they form the enamel close to the enamel-dentine junction (Pattern 1), and then produce enamel at a faster rate (Pattern 3), later slowing down towards the outside of the tooth (Pattern 1) before dying off.

The exact quantification of rate of formation of enamel is difficult and will require considerable further research, which will form part of my postdoctoral research. It is clear however that in hominoids all Pattern 3 enamel is fast formed, while Pattern 1 enamel is slowly formed.

The evidence from facets, grooves and longitudinal sections may be interpreted as follows. In all hominoids the slowly formed enamel close to the enamel-dentine junction is only 20 - 30 μm thick. This suggests that hominoid ameloblasts secrete enamel slowly, i.e. at less than 2 μm per day, for the first 10 - 20 days of activity. Only over the cusp tips do the ameloblasts continue to secrete enamel at this rate for a longer period. In human enamel ameloblasts form enamel at 5 - 6 μm per day for most of their life, slowing down only for the last few days before they die off. In Pan and Gorilla the ameloblasts secrete enamel at 5 - 6 μm per day to produce at least the first 60% of the enamel thickness in the region of maximum thickness. From this point on they form Pattern 1 enamel slowly at less than 2 μm per day. In absolute terms the ameloblasts produce about 500 - 600 μm of enamel at the fast rate, 5 - 6 μm per day, and only where this is equal or greater than the enamel thickness, i.e. more cervically, the enamel is of Pattern 3 cross section right up to the tooth surface.

In Pongo the ameloblasts form Pattern 3 enamel for most of their life at the rate of 5 - 6 μm per day. Typically they produce 750 - 1000 μm of enamel at this rate. This leaves an outer layer of enamel which has formed slowly, about 2.5 - 2.8 μm per day which is up to 350 μm

thick where the enamel thickness is at a maximum. In the zone of maximum thickness there is an outer layer of about 50 μm thick which has formed very slowly, at about 1.8 μm per day.

In Gibbons all of the enamel forms at 5 - 6 μm per day except for the outermost 20 - 30 μm. This is similar to the situation in man.

In Sivapithecus all of the enamel has formed quickly to within 20 - 30 μm of the outside of the tooth. It should be noted however, that in one specimen of S.sivalensis there was a zone of about 150 μm thickness which was Pattern 1 and therefore slowly formed. This situation was not typical for that tooth and certainly not for the genus and will be treated as exceptional until further specimens have been studied.

It is notable that in all hominoid species the areas with slowly formed enamel are areas in which no prism decussation is apparent. It is clear that areas of parallel prisms are more slowly formed than are areas of decussating prisms although the exact rate of formation can only be determined from cross striations. All of the great apes and man as well as Sivapithecus have Hunter-Schreger bands extending across the full width of the enamel in the cervical third of the crown. In all cases this is Pattern 3 enamel. No instances of slowly formed Pattern 3 enamel have been encountered. In the great apes and man the extent of the Hunter-Schreger bands in the more cuspal regions of the lateral enamel, where it is thickest, is variable. The maximum extent of the Hunter-Schreger bands is found in Sivapithecus and in

Homo. Hunter-Schreger bands extend about 750 - 1000 μm from the enamel-dentine junction in Pongo. In Pan and Gorilla the Hunter-Schreger bands were never found to extend for more than 500 - 600 μm from the enamel-dentine junction.

V. DISCUSSION

1. Introduction

Hominoid enamel is predominantly of Pattern 3 cross sectional type. This is the case for the deeper layers of enamel in all species as evidenced by studies of both developing and mature enamel, with the exception of the thin Pattern 1 layer immediately adjacent to the enamel-dentine junction. Homo, Hylobates and Sivapithecus have a thin outer layer of Pattern 1 enamel over the whole tooth surface reflecting the slowing down of ameloblasts prior to their dying off. Pongo has a thicker layer of Pattern 1 enamel but this is not a constant thickness over the whole tooth surface. Where the enamel is thickest the Pattern 1 layer may be up to 350 μm thick, and where the enamel is less than 800 μm thick the outer Pattern 1 layer is of the same thickness as is found in Homo, Hylobates and Sivapithecus. Pan and Gorilla have a very thick layer of Pattern 1 prisms where their enamel is thickest, up to 500 μm, but this layer is thinner where the enamel is thinner, moving cervically. When the enamel thickness is less than 500 μm the Pattern 1 layer is thin as in Homo, Sivapithecus and Hylobates.

2. The functional consequences of enamel microstructure

Enamel is not strictly divided into prismatic units. The discontinuities of the prism boundaries are not generally continuous with one another (see Figure 5.1). Prism boundaries rupture more easily than the continuous substance of the prism proper (Boyde,

1976). If cleavage is to occur through the boundary of the prisms then narrow isthimuses of tissue between adjacent prism boundaries have to be broken. Pattern 3 enamel cleaves by joining up the prism boundaries as the prism tails cannot pull out from between the heads because they are wider than their stems ("Keyhole" shaped). In a cross section of a Pattern 3 prism the crystals in the head portion are perpendicular to the cross section, i.e. parallel to the prism long axis, while the crystals in the tail section are fairly oblique. This means that to cleave Pattern 3 enamel across the heads of adjacent prisms requires the crystals in the tail portion to be broken. Even joining up prism boundaries of adjacent rows of prisms in Pattern 3 enamel requires the breaking of prism substance proper. In Pattern 1 enamel the prism boundaries are complete and the interprismatic region is separate from the prismatic regions. This means that cleavage can occur by joining up prism boundaries without breaking prism substance by cleaving apart the crystals in the interprismatic substance (Boyde, 1976). This means that cleavage requires less energy in Pattern 1 enamel than it does in Pattern 3 enamel (Boyde, 1976).

The tendency for enamel to cleave by separating along prism boundaries and by fracturing through prism tails or through interprismatic regions may be reduced by other structural features (Boyde, 1976). Enamel prisms show regular variations in thickness along their length (varicosities). These varicosities reflect daily variations in the rate of formation of enamel (Boyde, 1964). These varicosities interlock adjacent prisms and have the effect of

preventing shear in the longitudinal direction (i.e. along the long axis of the prisms). All of the hominoids studied showed prism varicosities (observed as cross striations) in both Pattern 1 and Pattern 3 enamel. A second structural feature which influences the ability of enamel to resist fracture is prism decussation. Enamel prisms do not extend straight from the enamel-dentine junction to the tooth surface but pursue wavy courses which cross over to a certain extent. This decussation is visible as Hunter-Schreger bands in hominoid Pattern 3 enamel. The decussation of the prisms does not exactly match the structure of plywood but the engineering effect on the strength of the material is much the same (Boyde, 1976). Prism decussation occurs when there is a marked change in the orientation of the Tomes' process pits (seen in developing enamel surface preparations) (Boyde, 1969b). Hunter-Schreger band formation was not observed in hominoid enamel with Pattern 1 cross section. This accords with the survey of mammalian orders by Boyde (1969b) in which he found no evidence of zone formation in Pattern 1 enamel in any order. The actual developmental reasons why this should be the case are unclear (Boyde, 1969b).

The implication of the microstructural evidence is that hominoids have a prism packing pattern (Pattern 3) which is resistant to cleavage. In Pan and Gorilla and to a lesser extent Pongo there is a considerable outer thickness of Pattern 1 enamel which fractures more easily than Pattern 3 enamel. This would render these teeth more liable to damage if very hard food objects, or hard non food inclusions, were chewed. Hylobates enamel has a Pattern 3 cross

section but shows a low degree of prism decussation which suggests that gibbon enamel would not be as strong as great ape and human enamel. In Pan and Gorilla teeth the prisms only decussate for about 60% of their length from the enamel-dentine junction. This means that as well as having an outer layer of Pattern 1 enamel this outer layer has no decussation and will therefore be more prone to fracture than the deep Pattern 3 enamel, with decussation, in these species. Homo and Sivapithecus have Pattern 3 enamel through most of the thickness and have decussation extending to close to the tooth surface. This means that their enamel is the best able to resist fracture of all hominoids.

3. Phylogeny of enamel microstructure

The deep layers of enamel shows the same structure in all hominoids. There is a thin layer of Pattern 1 enamel adjacent to the enamel dentine junction but the bulk of the deep enamel is Pattern 3. This Pattern 3 layer extends to within a short distance of the tooth surface in Homo, Hylobates and Sivapithecus. In Pongo the Pattern 3 enamel is overlain by a moderately thick layer (25 - 30%) of Pattern 1 enamel, and in Pan and Gorilla about 40% of the enamel thickness is Pattern 1. There are no major distinctions between the structure of the deep enamel in hominoids although Boyde and Martin (1983) indicated that they believe that further work on developing material may allow the definition of taxonomically useful subcategories of Pattern 3 enamel in hominoids. However, enamel structure is not constant in the outer layer of hominoid enamel.

The pattern found in the most distantly related members of the hominoid clade is also found in the largest number of genera and probably reflects the ancestral condition for Hominoidea. This is Pattern 3 enamel extending from close to the enamel-dentine junction to close to the tooth surface (Homo, Hylobates, Sivapithecus). Further work is required on gibbon enamel before the question of prism decussation can be definitely answered but it seems likely than the common ancestor of Hominoidea had poorly developed Hunter-Schreger bands as does Hylobates. The deviation from the ancestral condition seen in Pan and Gorilla, with a relatively great thickness of Pattern 1 enamel, links these species together. The relatively thin outer layer of Pattern 1 enamel in Pongo could be seen as a preliminary stage towards the African ape condition, but is better interpreted as an autapomorhic character in this genus. To interpret it otherwise would require either that the great apes form a clade or that the common ancestor of the great apes and man had enamel which differed in structure from the common ancestor of Hominoidea and that the ancestral condition was later re-evolved in the Homo clade, both of which are unlikely.

The taxonomic implications of enamel microstructure can be confused by sampling different depths and locations. In order to sample the typical prism packing type the deeper layers must be sampled. The actual depth from the tooth surface at which the typical structure is found will depend on the position, in terms of height up the crown, at which the structure is being sampled, and depth should more properly be defined from the enamel-dentine junction. This distribution

explains the discrepancy between the results obtained by Gantt et al (1977; Gantt, 1979) and those obtained by Vrba and Grine (1978a, 1978b) and Boyde and Martin (1982, 1983). Gantt's results correspond with those found in the outer, slowed down layer, for the great apes, an influence which does not affect the enamel in Homo or Sivapithecus. Vrba and Grine etched whole teeth and these preparations would reveal Pattern 3 enamel where the enamel is thinner but would be expected to produce Pattern 1 enamel where the enamel is thickest in the great apes. Unfortunately neither Gantt et al (1977) or Vrba and Grine (1978a, 1978b) specified the position at which they sampled enamel structure. Gantt (1979) deliberately sampled high lateral enamel which certainly accounts for the results he obtained. Had he sampled enamel more cervically then he would have found Pattern 3 enamel in all hominoids as he would effectively be sampling deeper enamel, i.e. enamel closer to the enamel-dentine junction.

The value of the enamel microstructure data for the present work is that it provides evidence as to the mechanism of development of the observed enamel thickness in hominoid species. These data were suggested to be the only way to resolve the polarity of enamel thickness changes in hominoid evolution (Chapter 4). The similar pattern of enamel microstructure distribution in Hylobates and Homo in teeth with very different thicknesses of enamel demonstrates the need to consider both sets of data. The two sets of data, enamel thickness and enamel microstructure, are considered in Chapter 6 and allow the recognition of ancestral conditions of enamel thickness for clades within the Hominoidea.

CHAPTER 6

DISCUSSION AND CONCLUSIONS

I. THE EVOLUTIONARY SIGNIFICANCE OF ENAMEL THICKNESS

1. The polarity of enamel thickness changes in hominoid evolution

Enamel thickness categories which take account of tooth size have been defined and their distribution among living hominoids has been documented in Chapter 4. Relative enamel thickness has been defined as average enamel thickness (c/e, Figure 4.1) expressed as a percentage of the square root of dentine area (b, Figure 4.1). The relative enamel thickness index has been used to define four size independent categories of enamel thickness metrically. Species with mean values of relative enamel thickness between 8.90 and 11.30 have thin enamel. Species with mean values of relative enamel thickness between 11.30 and 14.65 have intermediate/thin enamel. Species with mean values of relative enamel thickness between 14.65 and 17.25 have intermediate/thick enamel. Species with mean values of relative enamel thickness between 17.70 and 26.20 have thick enamel.

Thin enamel is found in Pan (8.90 - 11.30), Gorilla (9.15 - 10.93) and probably Hylobates (11.02). Intermediate/thick enamel is found in Pongo (14.65 - 17.21) and thick enamel is found in Homo (18.58 - 26.12). Sivapithecus specimens have thick enamel (17.73 - 21.69). The bracketed values are the 95% confidence limits of the mean. The condition of enamel thickness in the common ancestors of each hominoid clade could only be reliably determined for two nodes on the basis of the distribution of enamel thickness categories. Thin enamel is found in most primates and is probably the ancestral condition for the order. Thin enamel has also interpreted as the ancestral condition

for the anthropoid clade and for the catarrhine clade, as living members of these clades characteristically have thin enamel. Hylobates also has thin enamel so there are no reasons to doubt that the common ancestor of the Hominoidea had thin enamel (Chapter 4). Similarly, the presence of thin enamel in both Pan and Gorilla has been interpreted to mean that the common ancestor of the extant African apes had thin enamel. The condition of enamel thickness at the other nodes could not be determined as four explanations of these ancestral conditions appeared to be equally parsimonious (see Figure 4.29). Since enamel thickness is the product of the rate of formation of the enamel and the time during which the enamel was formed, it was suggested that microstructural evidence could be used to test the four hypotheses proposed for the condition of enamel thickness in the common ancestor of the great ape and human clade and in the common ancestor of the African ape and human clade (see Figure 4.29). The microstructural evidence was presented in Chapter 5.

The microstructural evidence revealed that hominoid enamel may develop at different rates at different stages of tooth crown formation. In Homo, Hylobates and Sivapithecus the enamel forms at the fast (Pattern 3) rate (5 - 7 μm per day) until just before the crown is completed when it slows down (Pattern 1) prior to the ameloblasts dying off. Pongo enamel is formed at the fast (Pattern 3) rate for most of the enamel thickness but has a rather greater thickness of slowly formed (Pattern 1) enamel at the outside of the tooth than do Homo, Sivapithecus and Hylobates. Pan and Gorilla form only about 60% of their enamel thickness at the fast (Pattern 3) rate

and the outer 40% forms at the slow (Pattern 1) rate.

This evidence has been interpreted to mean that the enamel thickness in Hylobates, Homo and Sivapithecus is only limited by the length of time during which the tooth crown is formed. This means that these taxa have the maximum thickness of enamel which can be produced by hominoid ameloblasts in the time during which the enamel is formed. In other words the thickness of enamel in Homo, Hylobates and Sivapithecus is determined by the developmental period of the teeth, and this is presumably related to maturation processes generally. In Pongo the ameloblasts slow down their secretory activity about two hundred microns before they die off at the tooth surface. If they continued to secrete enamel at the fast (Pattern 3) rate the enamel in Pongo would be somewhat thicker. In Pan and Gorilla the ameloblasts form the outer 40% of their enamel slowly (Pattern 1). If Pan and Gorilla ameloblasts continued to secrete their enamel at the fast (Pattern 3) rate this would result in teeth with much thicker enamel.

The hypotheses presented in Figure 4.29 can now be examined in turn combining the microstructural evidence with that of enamel thickness. Thin enamel has been interpreted as the condition of the common ancestors of the Primates clade, of the anthropoid clade, and of the catarrhine clade. It has been suggested that the common ancestor of the Hominoidea had thin enamel, as Hylobates also has thin enamel. Thin enamel can result either from the enamel forming quickly (Pattern 3) but for a relatively short period or from the enamel forming for a long period but at a slower average rate with a considerable portion

of Pattern 1 enamel. If the common ancestor of the hominoid clade had thin enamel which had formed slowly, i.e. with a relatively high proportion of slow formed (Pattern 1) enamel, then Hylobates would be derived in having thin enamel which has formed at the fast (Pattern 3) rate. This, in turn would mean that Hylobates enamel formed for a relatively shorter time than did the enamel in the common ancestor of Hominoidea. The more parsimonious interpretation is that the common ancestor of the Hominoidea had thin enamel which formed at the fast (Pattern 3) rate for most of its thickness. Hylobates would then retain the ancestral condition. (see Figure 6.1).

If the common ancestor of the great ape and human clade had thin enamel (Figure 4.29a) this could be either formed at the fast (Pattern 3) rate for a relatively short time or be formed relatively slowly but for a longer period of time. If the former were the case then the Pongo clade and the African ape and man clade would both have, independantly, evolved a relatively long period of tooth enamel formation. This would be a necessary consequence since the African apes have thin enamel which has formed relatively slowly but for a long period of time, and Pongo has intermediate/thick enamel, which has formed for a relatively long time, with about 70 - 75% forming at the fast (Pattern 3) rate, and because Homo has thick enamel which has formed for a relatively long time at the fast (Pattern 3) rate. If the interpretation that the common ancestor of the great apes and man had thin enamel which had formed for a relatively long time but at a relatively slow rate were correct, then this would mean that the common ancestor of the great apes and man developed enamel for a

relatively longer period of time than did the common ancestor of the Hominoidea, but the average rate at which the enamel was formed had slowed down. The consequences of this would be that Pongo has since reversed this process and evolved a longer period of enamel formation at the fast (Pattern 3) rate, and that Homo has reversed this pattern, in parallel, to develop thick enamel which all formed at the fast (Pattern 3) rate. Both of these explanations involve complex reversals of evolutionary polarity, and may, consequently, be considered to be falsified.

If the common ancestor of the great ape and human clade had intermediate/thick enamel (Figure 4.29c and 4.29d) then this could either be formed at the fast (Pattern 3) rate for most of its thickness or could be formed with about 25 - 30% of its thickness formed slowly (Pattern 1), as is the case in Pongo. If the first case were correct then it would imply that the orang-utan clade and the African ape and human clade had separately evolved a longer dental development period, with the rate of enamel formation in Pongo slowing down for the outer 25 - 30% and the rate of enamel formation in Pan and Gorilla slowing down for the outer 40% of the enamel thickness. If the common ancestor of the great ape and human clade had intermediate/thick enamel which had formed with the outer 25% forming relatively slowly (Pattern 1) then Pongo would retain this ancestral condition. However, this hypothesis would require that the common ancestor of the great ape and human clade had evolved a relatively long period of dental development and had slowed down the average rate of enamel formation with a substantial proportion of slow formed

(Pattern 1) enamel, and that the Homo clade had reversed this trend to maintain a constant fast (Pattern 3) rate of enamel formation. These interpretations require either an evolutionary reversal, or the parallel evolution of lengthened periods of tooth crown formation in the Pongo clade and in the African ape and man clade. The interpretation that the common ancestor of the great ape and human clade had intermediate/thick enamel is therefore considered to have been falsified.

If the common ancestor of the great ape and human clade had thick enamel then this would have formed at the fast (Pattern 3) rate, as no species with thick but slowly formed enamel have been documented. If the common ancestor of the great ape and human clade had thick enamel which had formed at the fast (Pattern 3) rate then there should be evidence of a small secondary reduction in enamel thickness in Pongo (which has intermediate/thick enamel), and of a considerable secondary reduction in enamel thickness in Pan and Gorilla (both of which have thin enamel). The microstructural evidence is that Pongo has mainly fast formed (Pattern 3) enamel but has about 25% of the thickness formed at the slow (Pattern 1) rate. This means that the enamel in Pongo would be somewhat thicker if its ameloblasts maintained a constant (Pattern 3) rate of enamel formation. Pan and Gorilla have about 60% of their enamel thickness formed at the fast (Pattern 3) rate, but the outer 40% in both genera has formed at the slow (Pattern 1) rate. This means that the enamel in Pan and Gorilla would be considerably thicker if their ameloblasts maintained the fast (Pattern 3) rate of enamel secretion. This evidence does not falsify the

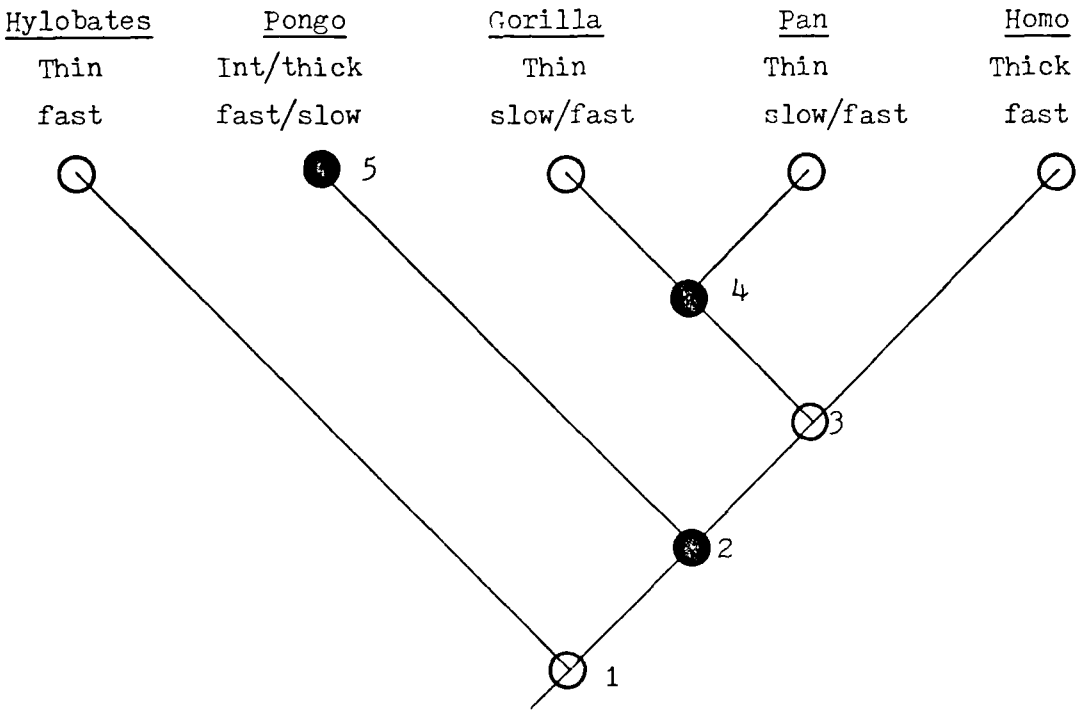
hypothesis that the common ancestor of the great apes and man had thick enamel.

If the common ancestor of the African apes and man had a different pattern of enamel thickness and microstructure than the common ancestor of the great apes and man, the only likely direction of change would be for the average rate of enamel formation to have been reduced. Any other interpretation would mean that man had re-evolved the enamel thickness and secretion rate seen in the common ancestor of the great ape and human clade from an ancestor with thicker enamel than seen in Homo. If the common ancestor of the African apes and man had evolved secondarily reduced enamel then man would have undergone a reversal and the average rate of enamel formation would have been secondarily increased. However, if the common ancestor of the African ape and man clade had thick, fast formed (Pattern 3) enamel, then the African apes would show evidence of a secondary reduction of enamel thickness. As discussed above, the microstructural data suggest that Pan and Gorilla would have substantially thicker enamel if their ameloblasts did not slow down their rate of secretion for the outer 40% of the enamel thickness. The possession of thin enamel, the outer 40% of which has formed slowly (Pattern 1), by both Pan and Gorilla means that the common ancestor of the African apes is best interpreted as having enamel thickness and structure as seen in Pan and Gorilla.

The enamel microstructure data do not falsify the hypothesis that the common ancestor of the great apes and man (and the common ancestor of

the African apes and man) had thick enamel and is in accordance with predictions based on those hypotheses regarding the rate of enamel formation in two separate branches of that clade. The hypothesis that the common ancestor of the great ape and human clade (and the common ancestor of the African ape and man clade) had thick enamel is the only hypothesis regarding the condition of enamel thickness at those nodes which cannot be falsified on the basis of the microstructural evidence regarding enamel development. This interpretation has therefore been adopted as the best available explanation for the distribution of enamel thickness categories in extant hominoids (Figure 6.1).

Figure 6.1: The polarity of enamel thickness and structure changes in hominoid evolution.



Node 1: Thin enamel, formed at the fast (Pattern 3) rate. The thin enamel is probab a retained primitive character.

Node 2: Thick enamel, formed at the fast (Pattern 3) rate. Thick enamel is a derived character, resulting from a relatively long period of tooth development.

Node 3: Primitive condition retained from node 2.

Node 4: Thin enamel, with about 40% of the enamel thickness formed at the slow (Pattern 1) rate. This is a shared derived character linking the African apes.

Node 5: Intermediate/thick enamel, with about 25% of the enamel thickness having formed at the slow (Pattern 1) rate. This is an autapomophic derived character at this node, derived with respect to node 2.

Homo, Hylobates, Pan and Gorilla retain primitive conditions of enamel structure and thickness from the ancestors representing node 3, node 1 and node 4 respectively.

Nodes at which the condition of enamel thickness and structure is a primitive retention are indicated by an open circle. Nodes at which the condition of enamel thickness and structure is a derived character are indicated by a black circle.

2. The taxonomic value of enamel thickness in hominoid evolution

The combination of the enamel thickness and enamel microstructure data for the interpretation of the polarity of enamel thickness changes in hominoid evolution (Figure 6.1) has a number of important implications. Firstly, the thin enamel category (as defined in the previous section) is not homogeneous. Hylobates, and probably the common ancestor of all extant hominoids had enamel which was thin because it formed for a relatively short period of time, although it formed at the fast (Pattern 3) rate. Pan and Gorilla have thin enamel because about 40% of their enamel thickness forms at a slow (Pattern 1) rate even though the whole of their enamel forms for a relatively longer period of time than does gibbon enamel. Similarly, the intermediate/thin and the intermediate/thick enamel categories could be heterogeneous. Both categories could have formed either at the fast (Pattern 3) rate, or could have formed a proportion of their thickness at the slow (Pattern 1) rate.

A fossil species with thin enamel which had formed at the fast (Pattern 3) rate could belong to the Hylobates clade; to a hominoid prior to the separation of the Hylobates clade from the great ape and human clade; or to a member of the great ape and human clade subsequent to the divergence of the gibbon clade but prior to the development of thick enamel in the common ancestor of the great ape and human clade. A fossil species with thin enamel that could be shown to be thin as a result of slowed down (Pattern 1) enamel development for a considerable proportion of its enamel thickness

would belong with the African ape clade.

No species, extant or fossil, have yet been shown to have intermediate/thin enamel, but a fossil species with this thickness of enamel would be interpreted to belong to an early stage of the African ape clade; or to an ancestral member of the great ape and human prior to the development of thick enamel in the common ancestor of the great apes and man, but subsequent to the separation of the Hylobates clade. The latter interpretation would require the enamel to be fast formed (Pattern 3) throughout its thickness, while the former interpretation would require the enamel to show a degree of secondary reduction with a percentage of slowly formed (Pattern 1) enamel thickness greater than is seen in Pongo, but less than is seen in the extant African apes.

A fossil species with intermediate/thick enamel could occupy three positions in hominoid phylogeny. Firstly, it could belong to the Pongo clade in which case it would have about 75% of the enamel thickness formed at the fast (Pattern 3) rate and about 25% of the enamel thickness formed at the slow (Pattern 1) rate. Secondly, it could belong to an early stage of the African ape clade, in which case the pattern of enamel microstructure distribution would be the same as for the first case. Thirdly, it could belong to an ancestral form of the great ape and human clade, in which case the enamel thickness would all be formed at the fast (Pattern 3) rate.

A fossil species with thick enamel, such as species of Sivapithecus,

could belong any part of the great ape and human clade subsequent to the divergence of the gibbon clade, with the exception of the African ape clade, and the later stages of the Pongo clade. Microstructural evidence would be unable to separate these alternatives.

It is clear that enamel thickness has little taxonomic value unless the development factors involved in its formation are also studied. These data would assist in the interpretation of fossil species with thin, intermediate/thin and intermediate/thick enamel. The least useful category of enamel thickness for taxonomic purposes is thick enamel, which appears to predominate among later Miocene hominoids.

In terms of the living hominoids, Hylobates retains the ancestral hominoid condition for enamel thickness and development. Homo retains the ancestral great ape and man clade condition for enamel thickness and development. Pongo has secondarily reduced enamel from the ancestral condition for the great ape and human clade. Pan and Gorilla have the most derived teeth showing a considerable degree of secondary reduction of enamel thickness.

II. THE RELATIONSHIPS OF THE LATER MIOCENE HOMINOIDEA

1. The polarity of characters

The cranial and dental characters which define the hominoid clade and contained clades are shown in Figure 6.2. This is not a definitive listing but concentrates on those characters which can be observed in later Miocene hominoids. The list is mainly based on characters discussed by Delson and Andrews (1975), Delson et al. (1977), Andrews and Cronin (1982), Harrison (1982) and Ward et al. (1983). In a number of important cases my interpretation of the polarity of characters differs from previous authors and these are discussed below.

a) Enamel thickness has been an important character for assessing the relationship of later Miocene hominoids. Usually thick enamel has been considered to be a derived character for the human clade and this has been a crucial element in the determination of the relationships of Sivapithecus (Kay and Simons, 1983). I have shown (above) that this position is not justified and I have determined the polarity of enamel thickness changes in hominoid evolution to be as shown in Figure 6.1.

b) A number of workers have proposed that greatly reduced molar cingula is a character which defines the great ape and human clade (Delson and Andrews, 1975). The tooth sections which I have prepared (Chapters 4 and 5) show that cingula are well developed in the African apes and especially in Gorilla. Molar cingula are variably developed

in Hylobates. The common ancestor of the Hominoidea probably had relatively well developed molar cingula though not as strongly developed as seen on Proconsul. Molar cingula have been completely lost in Pongo and in Homo but not in Gorilla or Pan. I have interpreted this to mean that the common ancestor of the great ape and human clade retained molar cingula (though not massively developed) and that they have been lost independently in the Pongo clade and in the human clade, as well as in parts of the Hylobates clade.

c) Robust mandibular corpora were interpreted by Kay and Simons (1983; Kay, 1982b) as a uniquely hominid adaptation, but the jaws of Pongo are more robust than those of African apes (Delson et al., 1977) so this interpretation may not be valid. The fact that robust jaws are commonly found in fossil species with thick enamel and are found in the extant species which have primitively retained relatively thick enamel suggests that robust jaws may be linked to the exaptive value of thick enamel. This feature is difficult to interpret as only Homo retains the primitive enamel thickness and structure condition for the great ape and human clade but it cannot be regarded as a uniquely human feature.

d) Gantt (1983) has suggested that Pattern 3B enamel is only found in members of the human clade. This result was not confirmed from a study of developmental material (Boyde and Martin, 1982, 1983) and its significance cannot be evaluated until further research is completed on developing enamel in great apes and humans.

e) Relatively high cheek tooth crowns with relatively low cusps have been interpreted as human features. In fact Pongo shows a similar tooth crown morphology and this morphology is an inevitable consequence of thickened enamel. Its presence in members of the human clade is therefore interpreted as a primitive retention.

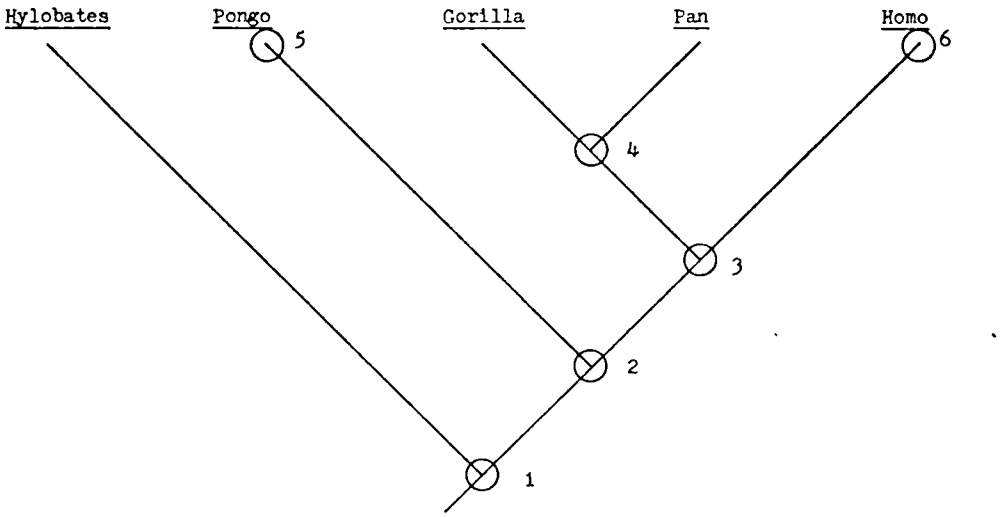
f) The structure of the mandibular symphysis of the common ancestor of the Hominoidea was probably with superior as well as inferior transvese torus (Harrison, 1982). The great ape and human clade is derived in having decreased the size of the superior torus (Figure 6.2).

g) It has been suggested that the maxillary canines in hominids have their long axes oriented from buccal to lingual (Kay and Simons, 1983). This character has been suggested to occur in Sivapithecus (Kay and Simons, 1983; Ward and Pilbeam, 1983) and has been interpreted as indicating the hominid affinities of Sivapithecus (Kay and Simons, 1983). However, the interpretation of this character is complicated as it appears to be related to the stage of wear of C^1 in Sivapithecus. Unworn Sivapithecus maxillary canines (e.g. GSI D-196, GSI D-299/300) have their long axes oriented from mesial to distal, as is the case in the extant great apes. I have interpreted this to mean that the C_1 long axis is not rotated in Sivapithecus, but that wear on the distal aspect of C^1 may result in a canine with the appearance of having a rotated long axis. Maxillary canines with rotated long axes are therefore interpreted as being specific to hominids and are not homologous with the structure in Sivapithecus,

which is related to wear.

The later Miocene hominoids are considered with reference to the characters and polarities shown in Figure 6.2.

Figure 6.2: Craniodental characters defining clades within the Hominoidea. With the exception of node 1 only derived characters are listed. Characters primitively retained at node 1 (from the common ancestor of Catarrhini) are listed if they are of importance at subsequent nodes in hominoid evolution.



Derived characters defining the hominoid clade (Node 1):

1) Pattern 3 enamel prism packing (Boyde and Martin, 19 2, 1983).
2) Palate relatively broad anteriorly (Harrison, 1982).
3) Upper I^1 low crowned and broad (Harrison, 1982).
4) I^2 modified from narrow conical shape (Delson and Andrews, 1975).
5) Incisors large relative to molars (Harrison, 1982).
6) P_3 with only moderate sized honing face (Harrison, 1982).
7) Trigon cusps quite rounded (Harrison, 1982).
8) Reduced cingulum on cheek teeth (this work).

Primitive characters retained at node 1:

2) Palate short and shallow anteriorly (McHenry et al., 1980).
2) Palate is deflected beneath premaxilla (Ward et al., 1983).
6) P_3 bilaterally compressed (Delson and Andrews, 1975).
9) Thin, fast formed, enamel (this work).
10) M^2 larger than or equal to M^1 greater than M^3 (Harrison, 1982).
11) Lower molars increase in size posteriorly.
12) Cheek tooth crowns with smooth enamel.
13) Cusps are relatively high (Andrews and Cronin, 1982).
14) I^2 slightly smaller than I^1 (Andrews and Cronin, 1982).
15) Upper premolars with buccal cusp higher than lingual.
16) Upper premolars short (mesial-distal) relative to molars.
17) P_4 is as long as it is broad (Harrison, 1982).
18) Canines high crowned and bilaterally compressed (Andrews and Cronin, 1982).

19) Moderate to high degree of canine sexual dimorphism.

20) Mandible deep and gracile (Andrews and Cronin, 1982 .

21) Mandibular tooth rows converge slightly anteriorly (Harrison, 1982).

22) Mandibular buttress reinforced by a superior and an inferior transverse torus (Harrison, 1982).

23) No development of supraorbital brow ridges (Harrison, 1982).

24) No fronto-ethmoidal sinus (Andrews and Cronin, 1982).

25) Orbits separated by broad septum (Cave, 1967, 1973).

26) Orbits as broad or broader than high (Andrews and Cronin, 1982).

27) Inferior orbital margin overlaps the superior margin of the nasal aperture (Harrison, 1982).

28) Nasal aperture ovoid, higher than broad (Harrison, 1982).

29) Nasal bones relatively short and narrow (Harrison, 1982).

30) Floor of nasal cavity truncated or stepped (Andrews and Cronin, 1982).

31) Zygomatic process shallow and not flaring (Andrews and Tekkaya, 1980).

32) Zygomatic foramina small and few in number (Andrews and Cronin, 1982).

33) No malar notch in inferolateral surface of zygomatic (Preuss, 1982).

34) Small incisive foramina (Andrews and Cronin, 1982).

35) No true incisive canal (Ward and Pilbeam, 1983).

36) Palatine foramina large and oval (Andrews and Cronin, 1982).

37) High dentine horns (this work).

Node 2:

2) Palate long and deep anteriorly (McHenry et al., 1980).

4) I^2 broad (Harrison, 1982).

6) P_3 broadened, reduced canine honing (Delson and Andrews, 1975).

9) Thick, fast formed (Pattern 3) enamel resulting from relatively long period of dental development (this work).

10) M^2 only slightly longer than M^1 (McHenry et al., 1980).

11) M_3 shortened and broadened with large hypoconulid (Delson and Andrews, 1975).

13) Cusps relatively low as a result of increased enamel thickness (this work).

15) Upper premolars with buccal cusp only slightly higher than lingual (Delson et al., 1977).

16) Upper premolars lengthened with respect to molars (Delson et al., 1977).

17) P_4 lengthened.

18) Canines robust (Andrews and Cronin, 1982).

20) ? Mandibular corpora robust ?

22) Inferior transverse torus well developed and dominant over superior torus (Harrison, 1982).

27) Inferior margin of orbits does not overlap the superior portion of the nasal aperture (Harrison, 1982).

28) Nasal aperture broad with flat inferior margin (McHenry et al., 1980; Harrison, 1982).

29) Nasal bones relatively long (Harrison, 1982).

Node 3:

23) Supra-orbital brow ridges developed.

24) Presence of fronto-ethmoidal sinus (Delson and Andrews, 1975).

35) Incisive fossa divided into two chambers by the vomeronasal contact with the hard palate being deflected beneath nasospinale resulting in the formation of a true incisive canal (Ward and Pilbeam, 1983).

36) Large sphenopalatine fossae (Andrews and Cronin, 1982).

Node 4:

9) Enamel secondarily reduced from thick to thin, with about 40% of the enamel thickness having Pattern 1 enamel prism packing (this work).

13) Cusps relatively high and pointed as a result of secondary reduction of enamel thickness.

20) Mandibular corpora deep and gracile (? derived ?).

Node 5:

2) Palate not deflected beneath premaxilla (Ward et al., 1983).

5) I^2 small compared to molar size, I^1 large relative to molar size.

8) Molar cingula reduced or absent.

9) Enamel secondarily reduced from thick to intermediate/thick with less than 25% of the thickness having Pattern 1 enamel prism packing (this work).

12) Strong wrinkling of crown enamel on cheek teeth (Delson et al., 1977).

14) I^1 much larger than I^2 (Andrews and Tekkaya, 1980).

20) Jaws robust (? derived ?) (Delson et al., 1977).

25) Interorbital distance reduced to a great extent (more even than in Pan paniscus) (Andrews and Cronin, 1982; Delson et al., 1977).

26) Orbits higher than broad (Andrews and Cronin, 1982).

29) Nasal bones relatively narrow (Delson et al., 1977).

30) Nasal cavity floor smooth and unstepped (Andrews and Cronin, 1982).

31) Deep and widely flaring zygomatic proceeses (Andrews and Tekkaya, 1980).

32) Zygomatic foramina above the level of the lower rim of the orbit, large and multiple (Andrews and Cronin, 1982).

33) Presence of a pronounced malar notch on the inferolateral aspect of the zygomatic (Preuss, 1982).

34) Restricted incisive foramen (Andrews and Cronin, 1982).

35) Incisive canal narrow (Ward et al., 1983).

36) Palatine foramen very narrow and slit like (Andrews and Cronin, 1982).

37) Relatively flat enamel-dentine junction (this work).

Node 6:

2) Maxillary dental arcade parabolic.

6) P_3 bicuspid, with metaconid (Kay, 1982b).

8) Reduced or absent molar cingula.

10) M^3 reduced morphologically and metrically.

11) M_3 smaller than M_2.

15) Upper premolars homomorphic with regard to cusp height.

18) Canines reduced in size and become incisiform. Long axis of C^1 cross section set buccolingually (Kay and Simons, 1983; Kay, 1982b).

19) Reduced canine sexual dimorphism.

20) Shallow, broad mandibles (? derived ?) (Andrews and Cronin, 1982).

21) Mandibular tooth row is parabolic.

22) Mandibular symphysis buttressed by external torus (chin).

23) Trend to reduce supraorbital brow ridges.

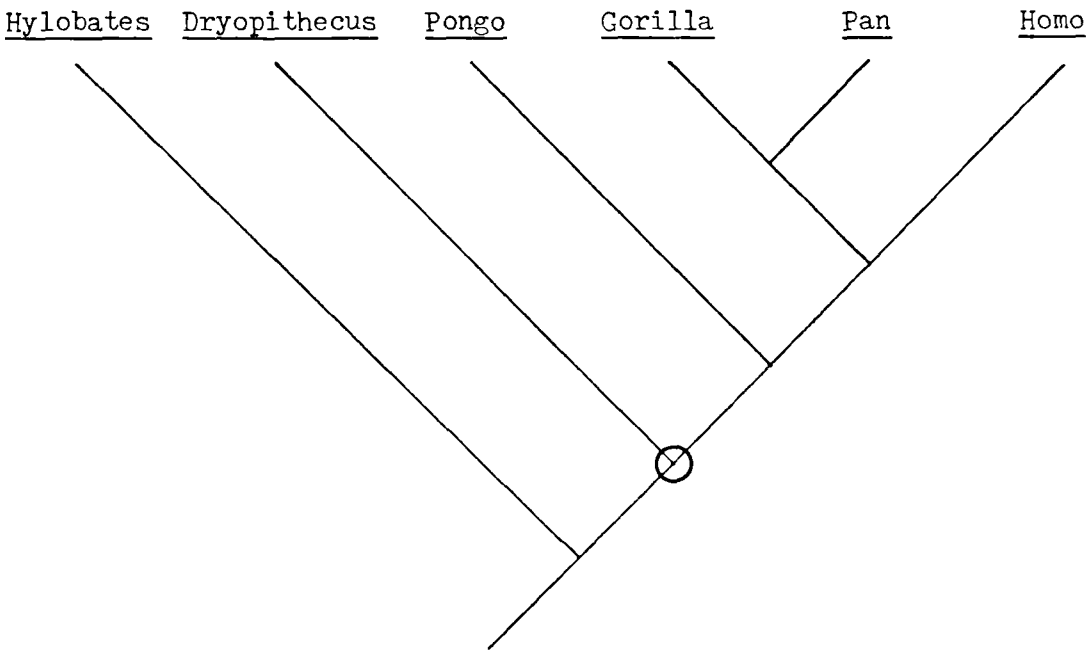
2. The cladistic relationships of Dryopithecus

a) Dryopithecus fontani and D.laietanus

These two species have been defined as size variants of a morphologically homogeneous sample from Western Europe (Chapter 3). Enamel thickness has not been metrically determined in any species of Dryopithecus, but on the basis of dentine exposure patterns Dryopithecus could have thin enamel, intermediate/thin enamel or possibly intermediate/thick enamel, but not thick enamel. On the basis of this evidence Dryopithecus could belong to the African ape clade, or possibly to the Pongo clade or to the hominoid clade prior to the development of thick enamel (see Figure 6.1). Dryopithecus does not possess a frontal-ethmoidal sinus which tends to exclude it from the African ape and human clade. Dryopithecus also retains a well developed superior transverse torus (Figure 6.2). The determination of the enamel thickness and enamel microstructure would confirm these interpretations (see Chapter 6, section I). It seems most likely therefore that Dryopithecus belongs to the hominoid clade but not to any part of the great ape and human clade.

Dryopithecus shows derived characters (Figure 6.2) which link it with the great apes and man rather than with the gibbons. The P_3 is broadened and less bilaterally compressed, and upper premolars are lengthened in proportion to molar length. Most significant, however, are the postcranial characters of the humerus of D.fontani from both St.Gaudens and Rudabanya, which are clearly shared derived characters with the great apes and man and which indicate that it is more closely

Figure 6.3: The cladistic relationships of Dryopithecus.



Shared derived characters at the node defining the clade comprising Homo, Pan, Gorilla, Pongo, and Dryopithecus. Character numbers refer to listing in Figure 6.2.

2) Palate long and deep anteriorly

6) P_3 broadened

11) M_3 broadened with large hypoconulid

16) Upper premolars lengthened with respect to molars

17) P_4 lengthened

18) Canines robu t

22) Inferior t a nsverse torus well developed, though not dominant over superior torus.

Most significant, however, are the postcranial characters of the humerus of D.fontani from both St.Gaudens and Rudabanya, which are clearly shared derived characters with the great apes and man (Figure 2.1) and which indicate that it is more closely related to man and the great apes than are the gibbons.

related to man and the great apes than are the gibbons. The retention of the primitive hominoid pattern in most other characters shows that Dryopithecus is less closely related to the living great apes than they are to each other, and in the absence of such evidence the two European species are best considered to be the sister group of the great ape and human clade rather than related to any one part of it (see Figure 6.3).

b) Saudi Arabian Dryopithecus

The Saudi Arabian material is similar in preserved parts to the European Dryopithecus. It is distinguished by retaining larger cingula on the upper molars than do specimens from Rudabanya and Spain and by having the buccal cusp on the upper premolars considerably higher than the lingual cusp. In terms of the size of P^3 and P^4 in relation to M^1 this material shows the great ape and human condition. The cladistic relationships of this material are therefore interpreted to be the same as in European Dryopithecus (Figure 6.3.).

c) "Sivapithecus" simonsi

The small amount of material assigned to this species is of uncertain affinities. As with Dryopithecus much of the dental morphology is primitive for the Hominoidea, and it lacks all of the derived features of Sivapithecus. The important difference is that simonsi has a P_3 which is very bilaterally compressed. This is interpreted as a primitive character for the Hominoidea (Delson and Andrews, 1975) (Figure 6.2) and is one of the features in which European Dryopithecus

is derived with respect to the common ancestor of the hominoid clade. The material assigned to simonsi cannot be shown to be more closely related to the great apes and man than are the gibbons. There is no evidence to show that simonsi could not represent a primitive gibbon, and it is hoped that the documentation of enamel thickness and microstructure for simonsi will provide evidence which will assist in the determination of its relationships. However, as Dryopithecus shares derived characters with great apes and man which are not found in simonsi the species cannot be considered to belong to that genus. It seems possible that the material represents a previously unknown genus, although I have suggested that the simonsi material would be conspecific with Hylopithecus hysudricus if the type of that species could be definitely determined to be a permanent tooth.

d) The Moroto palate

It was suggested in Chapter 3 that the Moroto material could not be referred to Proconsul and might represent a similar grade to Dryopithecus. The Moroto material has premolars which are as large relative to molar size as in Dryopithecus and is therefore more closely related to the great ape and human clade than are the gibbons and at least as closely as Dryopithecus. This material is not assigned to Dryopithecus because of the reported presence of a frontal-ethmoidal sinus, (Pilbeam, 1969), and if this is the case then the Moroto material belongs to a species which is more closely related to man and the African apes than is Pongo. The position of this material could be more precisely determined if enamel thickness and

enamel microstructure data were known, and its position in hominoid phylogeny is best left open at present. It seems probable to me that the Moroto material represents a new species, and possibly a new genus of hominoid.

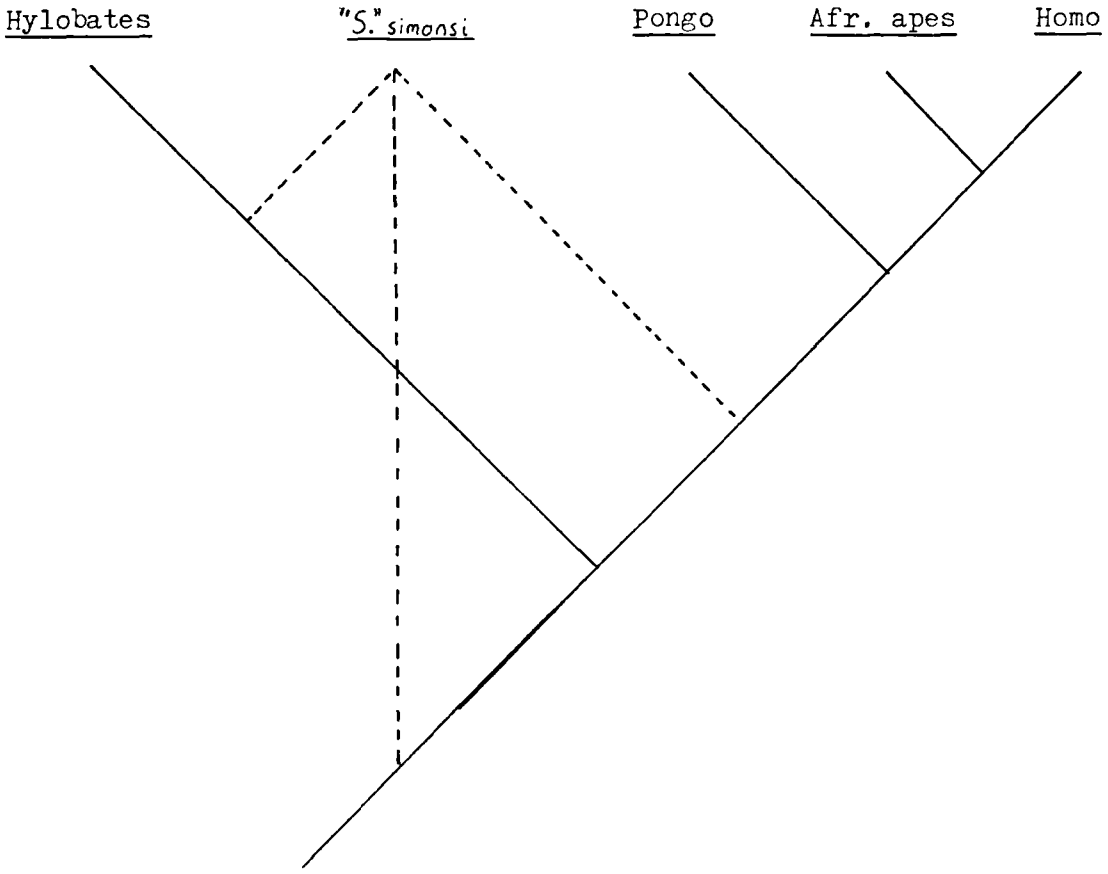
e) Summary

Three species of Dryopithecus, D.fontani, D.laietanus and a new species represented in Saudi Arabia, are more closely related to the great ape and human clade than are the gibbons but less closely related to the African ape and man clade than is Pongo. Dryopithecus is therefore interpreted to represent an early member of the great ape and human clade, prior to the development of thick enamel and prior to the last common ancestor of the extant great apes and man (Figure 6.3).

The material listed as "Sivapithecus" simonsi does not share any of the derived features which Dryopithecus shares with the great ape and man clade. This species could be related to a number of positions in hominoid phylogeny (Figure 6.4) as it retains the primitive hominoid morphotype in all known features.

The material known from Moroto shares derived characters with the great ape and human clade and with Dryopithecus. It may also share derived characters with the African ape and man clade which are known to be absent in Dryopithecus. These alternative explanations for the position of the species represented at Moroto could be resolved or at

Figure 6.4: Possible interpretations of the relationships of "Sivapithecus" simonsi.



The currently known hypodigm of "Sivapithecus" simonsi cannot be shown to share derived characters with the hominoid clade or with any part of that clade. Three possible explanations of its relationships are shown above. It is hoped that more detailed analysis, and additional material may be able to resolve these possibilities. "Sivapithecus" simonsi shares no derived characters with Sivapithecus, and is less closely related to the great ape and human clade than is Dryopithecus. This species cannot, therefore be assigned to either Sivapithecus or to Dryopithecus.

least narrowed down if the enamel thickness and enamel microstructure were known for the Moroto material (see Figure 6.1). The material from Moroto almost certainly represents a species which has not been named and probably a new genus also.

3. The cladistic relationships of Sivapithecus

a) Introduction

The five species of Sivapithecus recognised from Indo-Pakistan and Western Europe have thick, fast formed molar enamel. This character shows that they are more closely related to the great ape and human clade than is Dryopithecus. Within the great ape and human clade thick enamel has no taxonomic value except that it shows that Sivapithecus is not a member of the African ape clade (Figure 6.1).

b) Sivapithecus as a member of the human clade

The plesiomorphous character of thick enamel removes one of the three most significant characters used by Kay (1982b) to demonstrate a close relationship with hominids. The thick Pattern 3 enamel in man and Sivapithecus is undoubtedly homologous, but it has been shown above to be a shared primitive character from the great ape/man ancestral condition (Figure 6.1). Kay (1982a) also suggested that Sivapithecus shared a derived character with the human clade in having reduced C^1 sexual dimorphism. I have shown that his method of quantifying sexual dimorphism is inadequate (Chapter 2) and that in any case the largest and the smallest canines known from the Siwaliks can be shown to

belong to a single species, S.sivalensis (Chapter 3). The third crucial character for Kay and Simons (1983; Kay, 1982b) was the possession of robust mandibles. Pongo also has more robust mandibles than do the African apes (Delson et al., 1977) and the taxonomic value of this character within the great ape and human clade is questionable.

c) Sivapithecus as a member of the Pongo clade

A number of workers have proposed that Sivapithecus is more closely related to the orang-utan than are any living primates (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Lipson and Pilbeam, 1982; Ward and Pilbeam, 1983; Ward et al., 1983). Sivapithecus shows a number of characters which were interpreted as derived for Pongo (Figure 6.2.). These include:

I^1 much larger than I^2; this is certainly true for S.sivalensis and S.meteai although the central incisor is not as large in relation to M^1 size as in modern orang-utans.

Indistinct supraorbital torus; this is only known to be the case for S.sivalensis.

Interorbital distance reduced to an extent greater than in any living hominoid (including P.paniscus) except for Pongo; The degree of reduction does seem to be greater than is the case for Pan paniscus (Cramer, 1977). This character is known for S.sivalensis and S.meteai.

Orbits higher than broad; known only for S.sivalensis.

Nasal cavity floor smooth and unstepped; this character is known for S.sivalensis, and S.punjabicus (Ward et al., 1983) and S.meteai (Andrews and Cronin, 1982).

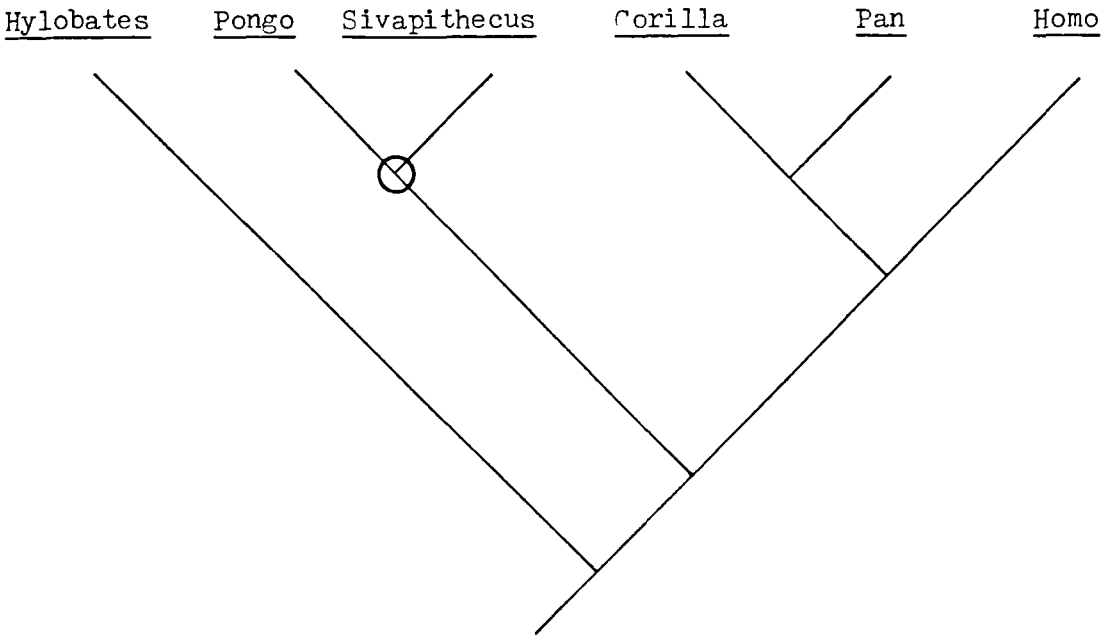
Sivapithecus meteai also shares restricted incisive foramina, and narrow palatine foramen with Pongo.

Relatively flat dentine surface; This character is known for S.sivalensis, S.punjabicus, S.darwini and S.alpani. The significance of this character is hard to determine and larger samples of fossil teeth need to be studied to demonstrate it clearly.

d) Discussion

Three species of Sivapithecus, S.sivalensis, S.punjabicus and S.meteai have been shown to share a number of derived characters with Pongo, although Pongo is still defined by some derived characters not seen, or known, in Sivapithecus (Figure 6.5). Two species, S.alpani and S.darwini, can only be shown to share one derived character with Pongo and with the other three better known species of Sivapithecus. These species are provisionally referred to Sivapithecus on the basis of their relatively flat dentine surface but further work is needed to clarify their position. These two species could represent a more primitive genus belonging to the orang-utan clade but this interpretation would require evidence relating to facial morphology yet to be discovered. The only derived character shared with hominids is the robust mandible in Sivapithecus. The value of this character

Figure 6.5: The cladistic relationships of Sivapithecus.



Shared derived characters at the node defining the clade comprising Pongo and Sivapithecus. Character numbers refer to the listing in Figure 6.2.

2) Palate not deflected beneath premaxilla.
14) I^1 much larger than I^2
25) Reduced interorbital distance.
26) Orbits higher than broad.
29) Nasal bones relatively narrow.
30) Nasal cavity floor smooth and unstepped.
31) Deep and widely flring zygomatic arches.
32) Zygomatic foramen large, but single in S.meteai.
34) Restricted incisive foramina.
35) Narrow incisive canal.
36) Palatine foramina very narrow and slit like.
37) Relatively flat enamel-dentine junction.

Characters which are derived in Pongo but in which the primitive condition is known to be retained in Sivapithecus.

5) I^1 very large relative to molar size.
8) Molar cingula reduced or absent (variable).
9) Enamel thickness secondarily reduced from thick to intermediate/thick.
12) Strong wrinkling of crown enamel.

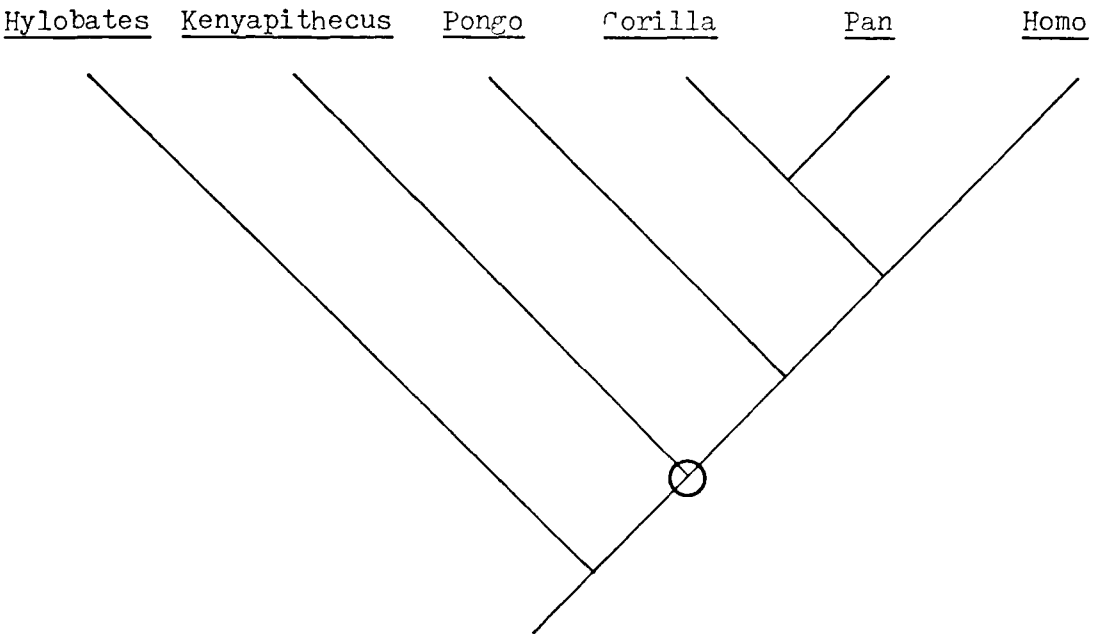
has been questioned and it does not out weigh the palatofacial evidence supporting the relationship of Siv pithecus with Pongo. The presence of robust mandibles in some undoubted members of the orang-utan clade, S.sivalensis and S.punjabicus, but not in S.meteai, further suggests that robust mandibles may have been evolved in more than one branch of the great ape and human clade or that this condition may be primitive for the great ape and human clade.

4. The cladistic relationships of Kenyapithecus africanus

On the basis of the dentine exposure pattern this species has been interpreted to have thick enamel. This feature allies Kenyapithecus with the great ape and human clade and shows that this genus is more closely related to the great ape and human clade than Dryopithecus. In addition Kenyapithecus shares a derived character of enlarged premolars relative to molar size with the clade comprising the great apes and man, Sivapithecus and Dryopithecus. The buccal cusp on the upper premolars is slightly higher than the lingual cusp, more similar to the situation in Dryopithecus than in Sivapithecus and the great ape and human clade. Another characteristic feature of Kenyapithecus is that it has very robust mandibular corpora. The interpretation of polarity of this character is problematic and it cannot presently be used to determine relationships.

With the exception of the somewhat heteromporphic cusp height in upper premolars Kenyapithecus could belong to any part of the great ape and human clade except to the African ape clade. It could also

Figure 6.6: The cladistic relationships of Kenyapithecus africanus.



Shared derived characters at the node defining the clade comprising Homo, Pan, Gorilla, Pongo, and Kenyapithecus. Character numbers refer to the listing in Figure 6.2.

6) P_3 broadened

9) Thick enamel, probably fast formed (Pattern 3) and resulting from a relatively long period of dental development.

13) Cusps relatively low as a result of increased enamel thickness.

16) Upper premolars lengthened with respect to molars.

17) P_4 Lengthened

18) Canines robust ?

20) Mandibular corpus robust (? derived ?)

22) Inferior transverse torus dominant over superior torus.

represent a form prior to the separation of the orang-utan from the African ape and human clade. These possibilities would be best assessed on the basis of enamel thickness, enamel microstructure and enamel-dentine junction morphology (see Figure 6.1). These data are not available at present so the relationships of Kenyapithecus remain ambiguous. For the present I have taken the position that Kenyapithecus is the sister group of the great ape and human clade because it has thick enamel, but retains the primitive condition of relative cusp height in upper premolars for hominoids (Figure 6.6). This position is by no means absolute but is not falsifiable on presently available data.

5. The cladistic relationships of Gigantopithecus

A number of workers have suggested that Gigantopithecus represents a primitive hominid as this genus shares a derived character, bicuspid P_3, with hominids. However, unlike hominids the C_1 in Gigantopithecus has been functionally incorporated into the postcanine grinding battery. With this morphology a unicuspid P_3 would be unlikely, and its presence in Gigantopithecus may reflect the increase in size of this taxon. In terms of dental morphology Gigantopithecus closely resembles Sivapithecus, and also Kenyapithecus. The position of Gigantopithecus cannot be determined on the basis of presently available evidence as it either retains characters which are primitive for the great ape and human clade or has derived characters which it shares with no other genus. I have provisionally interpreted Gigantopithecus to represent a specialised branch of the Pongo/Sivapithecus clade.

6. Summary

The relationships of the later Miocene hominoids are difficult to interpret in the absence of enamel thickness and enamel microstructure data. Many of the species of later Miocene hominoid appear to retain the primitive dental morphology from a common ancestor of the great ape and human clade subsequent to the divergence of the gibbon clade from the clade of great apes and humans. Two genera are sufficiently well represented and studied to allow a well supported interpretation of their relationships. These are Sivapithecus and Dryopithecus and the importance of adequate documentation of enamel structure and thickness in Sivapithecus, which has shown the polarity of change in enamel pattern, has enabled the relationships of this genus to be well established. Lack of such data makes it difficult to assign any of the other fossil taxa. Kenyapithecus is provisionally interpreted as the sister group of the great ape and human clade. (These relationships are shown in Figure 6.7). Gigantopithecus is suggested to represent a branch of the Pongo/ Sivapithecus clade but its position in this clade and its relationship to other members of the clade cannot be reliably determined at present. The material from Moroto is interpreted to represent a new species, and probably genus, which belongs to the clade comprising the great apes and man, Sivapithecus, Gigantopithecus, Kenyapithecus and Dryopithecus. The position of the taxon represented at Moroto within this clade is hard to determine in the absence of enamel data but the reported presence of a fronto-ethmoidal sinus (Pilbeam, 1969) implies a close relationship with the African ape and human clade. The Siwalik

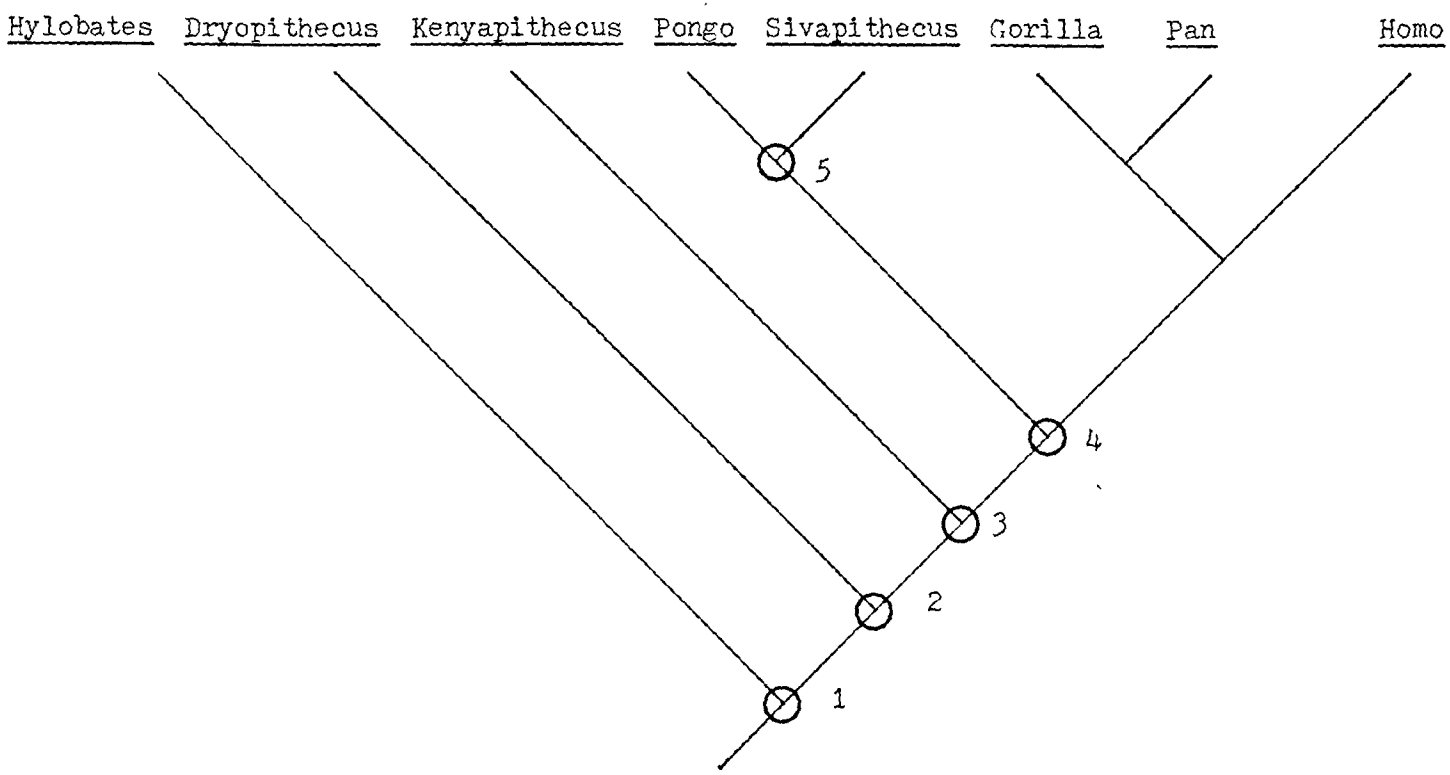


Figure 6.7: The cladistic relationships of the later Miocene Hominoidea.
Nodes 1 and 4 are defined as in Figure 6.2. Node 2 is as defined in Figure 6.3. Node 5 is as defined in Figure 6.5. Node 3 is defined by thick, fast formed (Pattern 3) enamel.

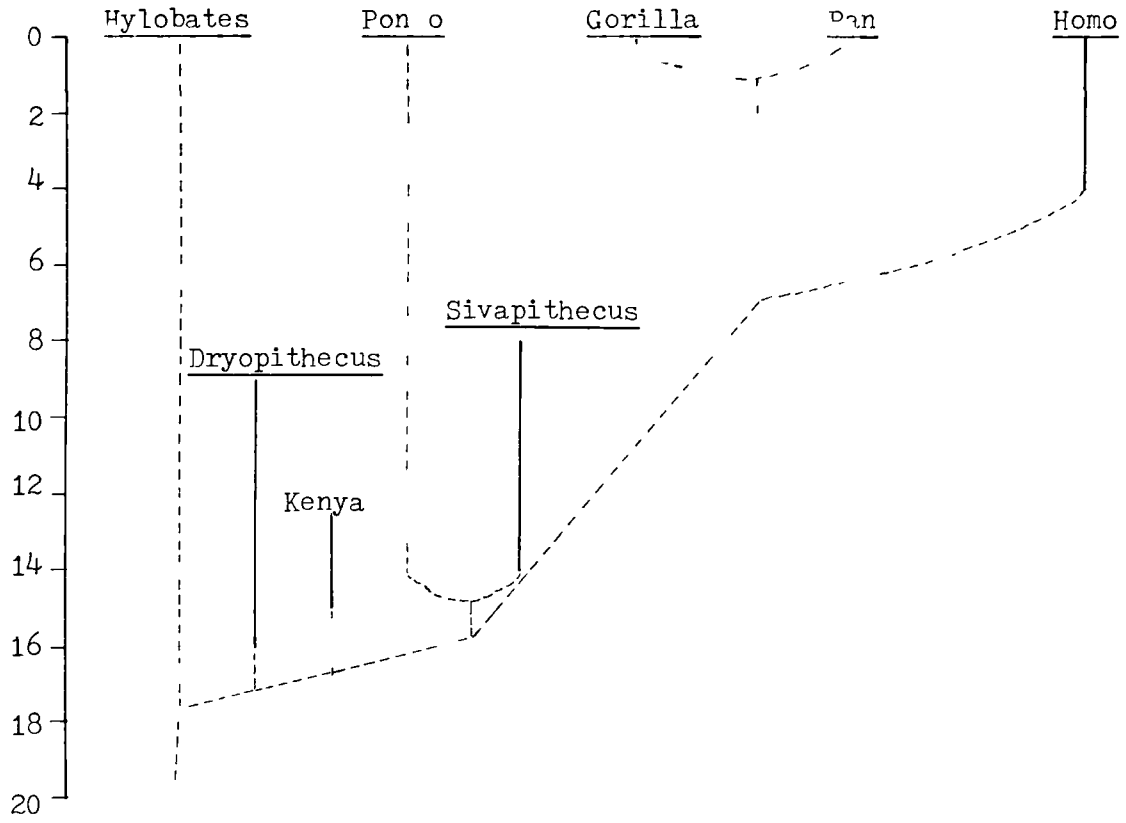
species simonsi cannot be reliably assigned to any higher taxonomic category. It shows no shared derived charaters with the great ape and human clade and could represent the sister group of the great ape, human and Dryopithecus clade, or could represent an early member of the Hylobates clade, or could represent the sister group of the Hominoidea. Until further material and/or more detailed analysis is carried out none of these possibilities can be refuted.

7. Phylogenetic implications

The phylogenetic implications of the relationships described above for Sivapithecus, Dryopithecus and Kenyapithecus are shown in a time related cladogram (Figure 6.8). Only Sivapithecus can be used to provide evidence regarding the dates of cladogenic events. On the basis of Siwalik material it is likely that Sivapithecus extends back in time to about 11 million years B.P. (Ward et al., 1983). If the species darwini and alpani have been correctly assigned to the orang-utan clade then this would show that the orang-utan had diverged from the African ape and man clade prior to 14 million years B.P. There is therefore good evidence that the Pongo clade had become distinct from the African ape and human clade before 11 million years ago and possibly before 14 million years ago.

With the exception of the Moroto material there is no evidence of hominoids which can be shown to belong to the African ape and human clade until the Plio-Pleistocene when members of the human branch of this clade can be identified. As a result of the present work it is clear that early members of the African ape and human clade, and indeed of the African ape clade, will have thick molar enamel with which has formed at the fast Pattern 3 rate. In the past specimens with thick enamel have been assumed to be hominids, but this can no longer be considered justified. It is clear that the tooth morphology seen in Kenyapithecus and Sivapithecus resembles the morphology in Homo, Paranthropus and Australopithecus because the hominids retain the primitive condition of thick enamel. It seems unlikely that a

Figure 6.8: The phylogenetic implications of the relationships of the later Miocene Hominoidea shown as a time related cladogram.



Notes: The time scale is in millions of years before present. Solid lines represent the approximately known geological age of taxa. The dates of the branching points are speculative as all of them could be much older than is shown. The upper limits for the dates of branching points have been determined in a number of cases:

1) Hominids are known from deposits around four million years old, this means that the branching point of the African ape clade from the human clade is older than that.
2) Sivapithecus is known from deposits of at least 11 - 12 million years (Ward et al., 1983) and the identification of Sivapithecus at Pasalar extends the range back to about 14 million years. This means that the Pongo clade separated from the African ape and man clade more than 14 million years before present.
3) Dryopithecus has been identified from the Dam formation of Saudi Arabia. This means that Dryopithecus is first recorded in beds about 16 million years old. As Dryopithecus is more closely related to man and the great apes than are the gibbons, this means that the Hylobates clade had separated from the great ape and human clade prior to 16 million years before present.

Kenya is used as an abbreviation for K nyapithecus, above.

thick enamelled ancestor of the African apes and man, or of the African apes alone, could be distinguished from early hominids on the basis of gross dental morphology.

III. THE FUNCTIONAL SIGNIFICANCE OF ENAMEL THICKNESS

1. Introduction

A number of models have been proposed to explain the similar dental morphology of australopithecines and ramapithecines. Because of the fragmentary nature of the Sivapithecus fossil record many workers have extrapolated the evidence relating to Australopithecus backward to Sivapithecus which was considered to have a broadly australopithecine masticatory apparatus. An important element in these models has been the presence of molar teeth with thick enamel, and this has usually been considered in conjunction with the robustly constructed jaws in attempts to provide dietary and/or behavioural models to explain the origin of these features.

Attempts to explain the functional significance of thick enamel in association with robust jaws began with the work of Jolly (1970a). He argued that the ramapithecine masticatory apparatus was adapted to generate large compressive forces or to permit extensive and frequent food preparation. Jolly (1970a) suggested that ramapithecines and australopithecines had a masticatory apparatus which equipped them for a diet centered on cereal grains (grass seeds). This model became known as the seed eating hypothesis although Jolly (personal communication) intended it to be generally applicable to hard food objects of relatively small size. Szalay (1972) has proposed a meat eating, scavenging theory to explain ramapithecine and australopithecine dental and gnathic adapations. He felt that these adaptations were most suited to a meat chewing or bone cracking

adaptation. Leopold and Ardrey (1972) argued that early hominids were meat eaters because they believed that toxic substances commonly found in many plants would tend to exclude them from hominid diets until the invention of cooking. This suggestion stimulated Coursey (1973) to argue that hominids may have eaten roots and tubers which generally contain relatively few toxic elements. Recently, Hatley and Kappelman (1980) have produced a compelling argument for the use of underground food resources by early hominids.

Most of these models were directed at explaining the dietary adaptations of australopithecines in a terrestrial setting, as implied by their bipedality. Simons and Pilbeam (1972; Simons, 1976) suggested that ramapithecines might also have had a ground feeding adaptive mode, as they had thick enamel like Australopithecus. In an extension of this argument Smith and Pilbeam (1980) suggested that because the arboreal orang-utan has thick enamel it may have passed through a terrestrial phase. The fact that Ramapithecus was considered to be the earliest hominid from 1961 onwards, and that it shared many australopithecine like dental and gnathic features, led many workers to extend these models back to explain the morphology in Ramapithecus. Since these models had all been developed to explain feeding adaptation of early hominids in an open country setting their application to Ramapithecus inevitably assumed some degree of terrestriality and open country living.

Walker (1979) has recently proposed that Australopithecus may in fact have eaten fruit as its enamel microwear patterns resembles those of

extant frugivores. Covert and Kay (1981) have also reported that the molars of Sivapithecus show that grass seeds were not an important part of its diet and that it avoided the inclusion of grit in food items. Kinzey (1974) showed that many features of the "Theropithecus complex" (Jolly, 1970a) could be found in arboreal primates which including tough food items in their diet. Kay (1981) suggested that enamel thickness was nothing directly to do with terrestriality and that it was in fact an adaptation to nut cracking, and that this food type was of greater significance than the environment in which it occured.

2. The functional significance of derived states of enamel thickness in hominoids

One drawback common to all of these models came to light as a result of the definition of thick enamel as the condition in the common ancestor of great apes and humans. The authors of the models mentioned above invariably assumed that they were trying to explain a uniquely hominid masticatory apparatus. The first place to attempt to address the adaptive significance of a character is at the node where it first appears, i.e. where it is a derived character. It must be remembered, however, that characters may not necessarily arise as an adaptation but may subsequently be incorporated into the adaptive strategy of the animal. If it can be shown that a character may be non-adaptive when it first appears one must look at the subsequent history of the character to determine whether it acquired exaptive significance. Primitive characters may be retained because they are still adaptive in the descendants or simply because they are neutral characters not selected against.

As far as enamel thickness is concerned only three nodes show derived states for the condition of the enamel in hominoids (Figure 6.1). Thick enamel is only a derived character for the node defining the great ape and human clade. Models to explain its retention in Australopithecus and Ramapithecus which incorporate bipedality and terrestriality are therefore inappropriate. The two other nodes at which the state of enamel thickness has been determined as derived are the common ancestor of Pan and Gorilla where it is thin as a result of

secondary reduction, and as an autapomorphic character in Pongo where it is slightly secondarily reduced.

The period of time during which teeth form is broadly related to the maturation period of the animal. It seems reasonable to interpret the lengthened period of enamel secretion in the great ape and human clade as the result of an increased growth period for the animal. This is in part related to body size, although the exact relationship has not yet been worked out. The effects of body size have been eliminated from the enamel thickness categories by scaling average enamel thickness with the square root of dentine area. For example, Gorilla has absolutely thicker enamel than does Pan, which means that Gorilla teeth form for a longer period than do Pan's, in relation to body size, but the relative enamel thickness index on which the categories of enamel thickness were based removes these size related differences. Therefore the thick enamel in the common ancestor of great apes and humans cannot be explained simply by size influenced periods of formation of each tooth. The evidence reported here suggests that the maturation period (for teeth particularly) is relatively longer in great apes and humans than in Hylobates and ancestral hominoids, so that the implication of thick enamel in the great ape and human clade is that it reflects a grade difference between ancestral hominoids and great ape and humans. It therefore seems entirely inappropriate to invoke dietary models to explain the appearance of thick enamel in hominoid evloution.

Thick enamel as it relates to great apes and humans must therefore be

regarded as an exaptation (Gould and Vrba, 1982). In other words it was not selected for any now existing function but became available for enchancing the fitness of the animal at a later stage. It is suggested that thick enamel came about as the result of a grade shift in the developmental period of the teeth in great apes and man. It may or may not have been adaptive at this stage, and at subsequent stages in hominoid evolution the presence of thick enamel opened up new dietary niches, but there is no reason to suppose that all great ape and human clade members shifted their dietary strategy in the same way to take advantage of the new niches. The evidence supports the interpretation that thick enamel was maintained in all branches of the great ape and human clade for a considerable period of time and that secondarily reduced enamel only evolved at a later stage in African ape evolution and in the evolution of the orang-utan. This may be interpreted to mean that thick enamel was either a neutral character or that its presence opened up new niches which were exploited and natural selection favoured the retention of thick enamel.

Most of the comparative evidence and the models used to explain the adaptive advantages of thick enamel in conjunction with robust jaws supports the interpretation that this exaptation allowed the species in which it was present to utilise food items which required prolonged mastication or the generation of large compressive forces. It has been suggested, however, that the facial architecture of Sivapithecus and Australopithecus does not support the interpretation of the generation of large compressive forces (Ward, personal communication). Ward suggests that the morphology is more consistent

with prolonged chewing which might be required for the utilisation of relatively low grade food items (Ward, personal communication). It seems likely, therefore, that the evolution of thick enamel in the great ape and human clade would have allowed members of this clade to exploit low grade food items which would not have previously been available to them. Many of these lower grade food items could be found in a non-forest environment, but thick enamel might also have contributed to species fitness in a forest environment by allowing the exploitation of hard rinded food objects (Kay, 1981). Thick enamel does not of itself provide the answer to these questions. The morphology of species with thick enamel must be considered in the light of palaeoecological data before the exploitation of non-forest environments can be established.

The presence of thin enamel in ancestral hominoids and in Hylobates is a retained primitive character. Thin enamel is a derived character in the African ape clade, and intermediate/thick enamel is a derived character in the Pongo clade, where it is secondarily reduced. Kay (1981) predicted that if an animal evolved thin enamel from an ancestor with thick enamel then this would denote a lineage moving away from a diet involving hard food objects towards a diet of leaves and soft fruit. Pan and Gorilla have secondarily reduced enamel thickness which has resulted in their having teeth in which shearing crests are much better developed than in any species with thick enamel. This secondary reduction took place subsequent to the separation of the African ape clade from the human clade

(Figure 6.1). This implies that thick enamel was selected against in the line leading to the African apes, perhaps in response to, and certainly with advantages for, the exploitation of the diet currently exploited by Pan and by Gorilla in particular. The fact that thick enamel was maintained in the lineage from the common ancestor of the great apes and man until after the separation of the African ape clade and the human clade implies that the selective factors which resulted in a secondary reduction of enamel thickness in African apes were not significant until after they had separated from the human clade. This may be interpreted to mean that the ancestors of the great ape and human clade and of the African ape and human clade were deriving some fitness benefit from the possession of thick enamel. The maintainance of thick enamel in this lineage may therefore mean that ancestral forms of great apes and man and of African apes and man were exploiting food resources for which teeth with thick enamel were adaptively advantageous.

The relatively small secondary reduction in enamel thickness in the Pongo lineage after its separation from the line leading to African apes and man is more difficult to interpret. The reduction in enamel thickness has not progressed to the extent that shearing crests are well developed and the diet of extant orang-utans does not indicate that thin enamelled teeth would be particularly advantageous. There are two possible explanations for this: firstly, the relatively small degree of secondary reduction of enamel thickness in Pongo could be interpreted to mean that selective forces favouring animals with thinner enamel have become important relatively recently; secondly, it

could mean that enamel has been secondarily reduced not because of any positive dietary advantage in thinner enamel but to reduce the demand for the mineral resources which would be required to develop thick enamel. Both of these interpretations have the implication that thick enamel is no longer selectively advantageous in Pongo, even if it had been advantageous in earlier stages of evolution in the Pongo clade.

It is concluded that thick enamel did confer exaptive advantages to ancestors of the African ape and human clade and was therefore maintained by natural selection. It seems likely that thick enamel was also maintained for some considerable time in the Pongo clade as species of Sivapithecus (see Section II above), which span several million years, show no sign of secondarily reduced enamel thickness. If this is the case then it is reasonable to assume that thick enamel had a selective advantage for the common ancestor of great apes and humans. It is further concluded that while thick enamel did not evolve in response to dietary pressures it became an important exaptation which was subequently maintained by natural selection. Sivapithecus, Australopithecus, Paranthropus, Homo and Kenyapithecus are the genera which have retained thick enamel and it presumably conferred selective advantages to some or all of them. It is from an understanding of the environment exploited by these genera that the exaptive advantage of thick enamel will be understood.

3. The environments in which thick enamel confers an exaptive advantage

Thick enamel is not maintained by natural selection in species whose diet consists predominantly of leaves and/or soft fruits. It is therefore unlikely that species in the great ape and human clade which retained thick enamel were exploiting these resources as a major component of their diet. It should be noted however, that thick enamel could be maintained in a soft fruit eating species where mineral resource availability, for the development of thick enamel, was not a critical factor.

The three extant genera of great apes provide evidence as to the type of diet and habitat in which thick enamel does not confer a selective advantage. In the case of Pongo enamel thickness reduction may not result from adaptation to a diet for which thick enamel is unsuitable but the diet of modern orang-utans is not one which requires the maintainance of thick enamel. In the case of the African apes it appears that thick enamel has been selected against to result in teeth with thin enamel. In the case of Gorilla, this reduction would seem to be a requirement for the development of teeth with well developed shearing crests which allow the exploitation of a diet of fibrous plant matter.

The palaeoenvironments in which hominoid genera which retained thick enamel; Kenyapithecus, Sivapithecus, Australopithecus, Paranthropus and Homo, have been the subject of several studies. The

palaeoenvironment with which Kenyapithecus is associated has been reconstructed as woodland-bushland (Andrews and Evans, 1979) and as open woodland/bushland (Pickford, 1983). The environment with which Sivapithecus is associated has been interpreted as a mosaic of forest, woodland and grassland (Badgley and Behrensmeyer, 1980). Andrews (1983) has reported that tropical forest settings are never indicated for Sivapithecus and has suggested that tropical to subtropical woodland settings with moderately seasonal climates and a single tree canopy are indicated. Andrews (1983) suggested that these environments would provide relatively abundant grasses in the ground vegetation and also geophytic plants with underground storage parts. Bernor (1983) has contrasted the subtropical and closed woodland settings of European Dryopithecus with the more open woodland setting with which Sivapithecus is associated. The environment of Australopithecus, Paranthropus and early Homo has been reconstructed as woodland-grassland or savanna (e.g. Andrews et al., 1979).

This evidence has usually been interpreted to mean that thick enamel is an adaptation to these more open environments and the exploitation of tougher food items. I have shown that thick enamel cannot be seen as an adaptation to these dietary categories, but the presence of thick enamel could have been an exaptation which allowed the exploitation of these environments. Andrews (1981) has suggested that newly emerged thick-enamelled hominoids could have expanded into less favourable woodland habitats as a result of competition with the expanding cercopithecoid monkey radiation. There is no evidence as to whether thick enamel appeared in ancestral great apes and humans prior

to this habitat shift or whether hominoids with less thick enamel made the shift which had consequences for their maturation period which resulted in their developing thick enamel. Whichever is the case it seems likely that thick enamel was an exaptation which enabled the great ape and human clade to successfully exploit the food resources in more open environments than had ancestral hominoids. It is also likely that the early ancestors of great apes and humans and of African apes and humans were were exploiting habitats significantly different to those exploited by living great apes. It is therefore possible that the secondary reduction in enamel thickness seen in the African apes and in the orang-utan is the result of their having secondarily moved back to tropical forest environments.

IV. CONCLUSIONS

Enamel thickness is best measured by dividing the area of the enamel cap exposed in a section through the cusp tips by the length of the enamel-dentine junction over which the enamel has developed. This produces an average enamel thickness which summarises the distribution of enamel over the whole tooth crown in the plane of section. An index of relative enamel thickness, which takes account of tooth size, has been developed by expressing average enamel thickness as a percentage of the square root of the area of dentine below the enamel-dentine junction. The relative enamel thickness index has been used to define four categories of enamel thickness metrically. Species with mean values of relative enamel thickness between 8.90 and 11.30 have thin enamel. Species with mean values of relative enamel thickness between 11.30 and 14.65 have intermediate/thin enamel. Species with mean values of relative enamel thickness between 14.65 and 17.25 have intermediate/thick enamel. Species with mean values of relative enamel thickness between 17.70 and 26.20 have thick enamel.

Thin enamel is found in Pan (8.90 - 11.30), Gorilla (9.15 - 10.93) and probably Hylobates (11.02). Intermediate/thick enamel is found in Pongo (14.65 - 17.21) and thick enamel is found in Homo (18.58 - 26.12). The bracketed values are the 95% confidence limits of the means. No species with intermediate/thin enamel have been encountered. Sivapithecus specimens, which provide the first published data on directly measured enamel thickness in three fossil species, have thick enamel (17.73 - 21.69).

On the basis of the distribution of enamel thickness in primates thin enamel is almost certainly the primitive condition for the Hominoidea. The condition of enamel thickness for the common ancestor of the great ape and human clade and for the common ancestor of the African ape and human clade cannot be reliably determined from the distribution of enamel thickness categories within these clades.

The pattern of dentine exposure resulting from tooth wear is not simply related to enamel thickness. It was proposed that wear in which dentine spots fuse together before dentine is exposed on each cusp be termed dentine fusion wear (previously this has been known as "thick-enamelled" wear). Wear in which dentine spots appear separately on each cusp before joining up should be called dentine separation wear (previously termed "thin-enamelled" wear). Dentine fusion wear is only found in species with thick enamel, but dentine separation wear is found in species with thin, intermediate/thick and probably intermediate/thin enamel. The use of the term "thin-enamelled" wear lumps these three categories together which is misleading. On the basis of the dentine exposure pattern Gigantopithecus, Kenyapithecus and Sivapithecus meteai have been determined to have thick enamel. Dryopithecus teeth wear with dentine separation and may therefore have thin, intermediate/thin or intermediate/thick enamel.

A correlation was found between the rate at which hominoid enamel is formed and the enamel prism packing pattern which results. Enamel prisms exhibit cross striations in longitudinal section which

correspond with 24 hours of enamel formation. Pattern 1 enamel was found to be associated with a cross striation repeat interval of less than 2 μm. Pattern 3 enamel was found to be associated with a cross striation repeat interval of 5 - 7 μm. In other words Pattern 3 enamel is formed at about three times the daily rate of Pattern 1 enamel in hominoids. Prism decussation, as evidenced by Hunter-Schreger band formation, was found only in fast formed (Pattern 3) enamel.

All species of hominoid studied had a thin layer of slowly formed (Pattern 1) enamel immediately adjacent to the enamel-dentine junction, and all hominoids had a layer of slowly formed (Pattern 1) enamel towards the outside of the tooth. The thickness of the outer layer of slowly formed enamel (Pattern 1) varied considerably in the hominoids studied. With the exception of the layer adjacent to the enamel-dentine junction, all of the hominoids studied have predominantly fast formed (Pattern 3) enamel in the deep layers of enamel. This result was obtained for both mature and developing enamel surface preparations. Three categories of enamel structure distribution were found. In Homo, Hylobates and Sivapithecus the fast formed (Pattern 3) enamel extends to within a short distance of the tooth surface. In Pongo the Pattern 3 enamel is overlain by a moderately thick layer (25 - 30%) of slowly formed (Pattern 1) enamel. In Pan and Gorilla the Pattern 3 enamel is overlain by a thick layer (about 40%) of slowly formed (Pattern 1) enamel.

The distribution of enamel prism packing patterns found in the most

distantly related members of the hominoid clade is also found in the largest number of genera and probably reflects the ancestral condition for the Hominoidea. This is having fast formed (Pattern 3) enamel extending from close to the enamel-dentine junction to close to the tooth surface. The deviation from the ancestral condition seen in Pan and Gorilla, with a relatively high proportion of slowly formed (Pattern 1) enamel towards the outside of the tooth, links these taxa together. The relatively thin outer layer of slowly formed (Pattern 1) enamel in Pongo could be seen as a preliminary stage towards the African ape condition, but is better interpreted as an autapomorphic character in this genus. To interpret it otherwise would require evolutionary reversals for which there is no evidence.

These results have major consequences for the interpretation of enamel thickness categories. The thin enamel in Hylobates is not homologous with the thin enamel in Pan and Gorilla. Hylobates has enamel which is thin because it is formed for a relatively short period while Pan and Gorilla have enamel which is thin because it forms at a relatively slow (average) rate. If Pan and Gorilla developed their whole enamel thickness at the fast (Pattern 3) rate, which is primitive for Hominoidea, then they would have much thicker enamel. Similarly if Pongo ameloblasts did not slow down their secretory rate for the development of the outer 25 - 30% of the enamel thickness then the enamel would be somewhat thicker.

This evidence was interpreted to mean that the common ancestor of Hominoidea had thin enamel which had formed at the fast (Pattern 3)

rate, but for a relatively short time. The common ancestor of the great ape and human clade had thick enamel which had formed at the fast (Pattern 3) rate for a relatively longer time than in the common ancestor of the Hominoidea. Pongo has secondarily reduced enamel thickness (from thick to intermediate/thick) as a result of ameloblasts slowing down enamel formation for a greater portion of their activity than was the case for the common ancestor of the great ape and human clade. The common ancestor of the African ape and human clade had thick enamel which formed at the fast (Pattern 3) rate. This is a primitive retention from the common ancestor of the great ape and human clade. Pan and Gorilla share a derived character of secondarily reduced enamel thickness (from thick to thin) as a result of their ameloblasts slowing down their secretory rate for a large proportion of their life. Homo retains thick enamel from the common ancestor of the great ape and human clade, because its ameloblasts retain the primitive fast (Pattern 3) rate of enamel formation for most of their activity.

Thick enamel is therefore a derived character which defines the clade comprising the great apes and man. Thick enamel is the result of teeth developing for a relatively longer period in members of the great ape and human clade than was the case for the common ancestor of the hominoid clade. Thick enamel is best interpreted as the result of a grade shift in the development period of the teeth, and dietary models to explain the evolution of thick enamel are therefore inappropriate. However, thick enamel may be seen as an exaptation which subsequently conferred increased fitness on the species in which

it developed. The retention of thick enamel for long periods of time may be interpreted to mean that thick enamel had exaptive value, but alternatively could mean that it was a neutral character which was not selected against.

A fossil species with thick enamel which formed at the fast (Pattern 3) rate shares a derived character with the great ape and human clade. Such a species could belong to any part of that clade with the exception of the African ape clade and later stages of the Pongo clade. Equally, thick enamel could be found in a species prior to the separation of the Pongo clade from the African ape and human clade. The presence of thick enamel in a fossil species is of limited value for determining relationships within the great ape and human clade. Sivapithecus specimens all had thick enamel which had developed at the fast (Pattern 3) rate. On the basis of this character they are more closely related to the great ape and human clade than are the gibbons but could belong to any part of that clade with the exception of the African ape clade. Kenyapithecus and Gigantopithecus were interpreted to have thick enamel on the basis of their molars showing dentine fusion wear, but no metrical or developmental data are available. The determination of their relationships on the basis of enamel thickness is the same as for Sivapithecus.

A fossil species with intermediate/thick enamel could belong to three positions in hominoid phylogeny. Firstly, it could represent a species more closely related to the great ape and man clade than Hylobates but a stage in the evolution of this clade prior to the

cladogenesis of the Pongo clade and of the African ape and man clade. Secondly, it could be closely related to Pongo, sharing a derived character of secondarily reduced enamel thickness (from thick to intermediate/thick). Thirdly, it could represent an early member of the African ape clade prior to the secondary reduction of enamel to thin enamel. Microstructural evidence would allow the distinction of the first possibility from the second and third. If the enamel were found to have developed at the fast (Pattern 3) rate then the species would be sampling a stage of hominoid phylogeny subsequent to the cladogenesis of the Hylobates clade, but prior to the separation of the Pongo clade from the African ape and man clade. If the enamel showed evidence of being secondarily reduced (from thick to intermediate/thick, i.e. if it had a relatively great outer thickness of slowly formed (Pattern 1) enamel) then it could belong to an early stage of the African ape clade or to the Pongo clade.

A fossil species with intermediate/thin enamel could occupy two positions in hominoid phylogeny. Firstly, it could represent an ancestral form of the great ape and human clade subsequent to the cladogenesis of the Hylobates clade. Secondly, it could represent an early member of the African ape clade. Microstructural evidence would allow the recognition as to which of these interpretations was correct. If the enamel were found to have developed at the fast (Pattern 3) rate then position 1 would be correct. If, on the other hand, the enamel showed evidence of being secondarily reduced from thick to intermediate/thin then the species would belong to an early stage of the African ape clade.

A fossil species with thin enamel could belong to four positions in hominoid phylogeny. Firstly, it could represent the sister group of Hominoidea. Secondly, it could represent part of the Hylobates clade. Thirdly, it could represent an ancestral form of the great ape and human clade subsequent to the cladogenesis of the Hylobates clade but prior to the separation of the Pongo clade from African ape and human clade. Fourthly, it could belong to the African ape clade. Microstructural evidence would permit the distinction of the fourth possibility from the other three. If the enamel were found to have a relatively great outer thickness of slowly formed (Pattern 1) enamel then the fossil would belong to the African ape clade. If the enamel had developed at the fast (Pattern 3) rate then any of the first three positions in hominoid phylogeny would be possible.

Enamel thickness is therefore a useful diagnostic tool for the determination of the relationships of fossil species. Its diagnostic value is greatly increased when the thickness is considered in conjunction with microstructural evidence regarding the rate at which the enamel thickness has been developed.

Dryopithecus species have teeth which wear with the dentine separation pattern. It is probable that they do not have thick enamel, but this pattern of dentine exposure could be found in species with thin, intermediate/thin or intermediate/thick enamel. On the basis of examination of naturally fractured teeth it was considered likely that Dryopithecus has either thin or intermediate/thin enamel. As discussed above this could imply membership of the African ape clade

or that Dryopithecus is less closely related to the African ape and human clade than is Pongo. The position of Dryopithecus in hominoid phylogeny could be much more precisely determined if specimens become available for sectioning which would allow the collection of enamel thickness and enamel microstructure data. Unfortunately this has not been possible for the present work.

In the absence of enamel thickness and enamel microstructure data the relationship of Dryopithecus to other hominoids has been determined on the basis of cranio-dental morphology. Similarly, the documented enamel thickness and enamel microstructure in Sivapithecus does not permit the exact determination of its relationships. Sivapithecus retains the ancestral condition of enamel thickness and enamel microstructure reconstructed for the common ancestor of the great ape and human clade. This pattern does not preclude its being related to any part of the great ape and human clade with the exception of the African ape clade. However, the reliance which has formerly been placed on thick enamel as indicating particularly affinity with hominids is not justified.

On the grounds of cranio-facial morphology three species of Sivapithecus; S.sivalensis, S.punjabicus and S.meteai can be shown to share derived characters with the orang-utan. These morphological areas are not known for the species darwini and alpani, but these taxa appear to share one derived character, a relatively flat dentine-enamel junction, with Pongo and the three other species of Sivapithecus, and they have been assigned to Sivapithecus on that

basis. Sivapithecus is considered to be the sister group of Pongo.

Kenyapithecus shares derived characters with the great ape and human clade but shows no derived characters which distinguish it from the hypothetical common ancestor of that clade. Kenyapithecus africanus is provisionally interpreted to be the sister group of the great ape and human clade. Gigantopithecus shares derived characters with the great ape and human clade, but where it shows derived characters from the ancestral condition for that clade these are not shared with any other taxon. On the basis of the similarity in morhology of Gigantopithecus with the Sivapithecus species from Indo-Pakistan it is suggested that Gigantopithecus be considered to belong to the Pongo/ Sivapithecus clade.

The material belonging to the species simonsi cannot be shown to exhibit any derived characters to distinguish it from the common ancestor of the Hominoidea. Its relationships cannot be precisely determined on this basis but it is clearly less closely related to the great ape and human clade than are Kenyapithecus or Dryopithecus. The material from Moroto, Uganda, shares derived characters with the great ape and human clade and has been reported to share derived characters with the African ape and human clade. This material appears to represent a new species and genus but its relationships to other hominoids cannot be precisely determined at present. Three species of Dryopithecus; D.fontani, D.laietanus and an unnamed species from

Saudi Arabia, share derived dental characters with the great ape and human clade. D.fontani lacks a fronto-ethmoidal sinus which would tend to exclude it from the African ape clade, and none of the Dryopithecus species has thick enamel which probably excludes them from any other part of the great ape and human clade. Dryopithecus is interpreted as the sister group of the clade comprising Pan, Gorilla, Homo, Pongo, Sivapithecus, Gigantopithecus and Kenyapithecus. These interpretations of the relationships of the later Miocene hominoids are shown in Figures 6.7 and 6.8.

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APPENDIX A

ENAMEL THICKNESS MEASUREMENTS AND SAMPLE DATA

Pan troglodytes: Enamel thickness sample data.

ID.	Tooth type	Sex	M-DC	B-LC	M-DCxB-LC	Museum no.
Pa 1	Right M^1	M	-	-	-	M 2a
Pa 2	Right M^2	M	10.6	12.1	128.3	M 2a
Pa 3	Right M^3	M	9.2	10.8	99.4	M 2a
Pa 4	Right M^1	M	10.3	11.3	116.4	M 1939-3385
Pa 5	Left M^2	M	11.6	13.8	160.1	M 1939-995
Pa 6	Left M^3	M	10.2	12.5	127.5	M 1939-995
Pa 7	Right M_1	M	10.9	10.4	113.4	M 1939-3385
Pa 8	Right M_2	M	11.6	10.7	124.1	M 1939-3385
Pa 9	Right M_3	M	11.3	10.2	115.3	M 1939-3385
Pa 10	Left M_1	M	11.5	10.4	119.6	M 1939-1001
Pa 11	Right M_2	M	12.2	11.8	144.0	M 2a
Pa 12	Left M_3	M	10.1	9.9	100.0	M 2a
Pa 13	Left M^1	F	10.2	12.1	123.4	M 1939-3373
Pa 14	Left M^2	F	10.0	11.1	111.0	M 1939-3373
Pa 15	-	-	-	-	-	-
Pa 16	Right M^1	F	11.1	12.9	143.2	M 1939-3387
Pa 17	Right M^2	F	11.1	12.5	138.8	M 1939-3387
Pa 18	-	-	-	-	-	-
Pa 19	Right M_1	F	11.1	10.2	113.2	M 1939-3373
Pa 20	Right M_2	F	11.4	10.5	116.3	M 1939-3373
Pa 21	Right M_3	F	8.9	9.4	83.7	M 1939-3373
Pa 22	Right M_1	F	12.1	11.3	136.7	M 1939-3387
Pa 23	Right M_2	F	13.2	11.4	150.5	M 1939-3387
Pa 24	-	-	-	-	-	-

Notes: M-DC - mesial to distal crown length

B-LC = buccal to lingual crown breadth.

Enamel thickness measurements from buccal to lingual sections through the mesial cusps of Pan troglodytes molars (see Figures 4.1 and 4.2 for explanation of the position and orientation of the measurements).

	Pa 1 M^1	Pa 4 M^1	Pa 16 M^1	Pa 2 M^2	Pa 5 M^2	Pa 17 M^2	Pa 6 M^3	M^1 Mean	M^2 Mean	M^3 Mean
a)	-	52.5	66.5	48.0	58.5	56.4	49.1	59.5	54.3	-
b)	-	42.7	54.9	34.3	47.6	42.4	40.0	48.8	41.4	-
c)	-	9.8+	11.6+	13.7	10.9+	14.0	9.1+	10.7	12.9	-
d)	-	21.8	25.7	20.9	21.9	22.5	20.9	23.8	21.8	-
e)	-	21.3	22.3	19.2	20.4	20.8	19.4	21.8	20.1	-
f)	0.06*	0.47+	0.41	0.24*	0.59	0.47	0.53	0.44	0.53	-
g)	0.00*	0.35	0.24	0.35+	0.35	0.53	0.35	0.30	0.44	-
h)	0.55+	0.51	0.40	0.73	0.63	0.73	0.57	0.49	0.70	-
i)	0.53+	0.50	0.50	0.70	0.57	0.60	0.57	0.51	0.62	-
j)	0.71	0.65	0.53	0.65	0.65	0.71	0.35	0.63	0.67	-
k)	0.85	0.67	0.64	0.63	0.91	0.59	0.65	0.72	0.71	-
l)	1.11	0.67	0.70	0.83	0.61	0.98	0.73	0.83	0.81	-
m)	0.90	0.83	0.66	0.63	0.94	0.60	0.68	0.80	0.72	-
n)	1.23	0.67	0.93	0.97	(1.36)	0.98	0.97	0.94	0.98	-
o)	2.01	2.18+	2.01	2.36	1.42	1.53	1.77	2.07	1.77	-
p)	2.01	2.24	2.18	2.24	1.65	1.47	1.95	2.14	1.79	-
c/b	-	0.23+	0.21+	0.40	0.23+	0.33	0.23+	0.22	0.32	-
c/e	-	0.46+	0.52+	0.71	0.53+	0.67	0.47+	0.49	0.64	-
d/e	-	1.02	1.15	1.09	1.07	1.08	1.08	1.09	1.08	-

	Pa 10 M_1	Pa 19 M_1	Pa 22 M_1	Pa 8 M_2	Pa 11 M_2	Pa 20 M_2	Pa 23 M_2	Pa 12 M_3	Pa 21 M_3	M_1 Mean	M_2 Mean	M_3 Mean
a)	38.8	37.6	48.9	46.2	51.4	43.2	51.3	-	29.1	41.8	48.0	-
b)	27.7	27.5	37.5	33.9	37.5	31.6	37.5	-	22.3	30.9	35.1	-
c)	11.1	10.1+	11.4+	12.3+	13.9	11.6	13.8	-	6.8+	10.9	12.9	-
d)	18.9	18.8	20.6	21.4	21.1	20.4	21.3	-	16.5	19.4	21.1	-
e)	15.9	16.7	19.2	19.1	19.3	18.9	18.6	-	14.9	17.3	19.0	-
f)	0.77	0.30*	0.35*	0.47+	0.41+	0.61	0.83	0.35	0.41+	0.47+	0.58	0.38
g)	0.47	0.59	0.41+	0.47	0.53	0.74	0.53	0.38	0.65	0.49	0.57	0.52
h)	0.52	0.74	0.71	0.58	0.63	0.81	0.71	0.66	0.54	0.66	0.68	0.60
i)	0.51	0.59	0.60	0.48	0.81	0.60	0.71	0.72	0.70	0.57	0.65	0.71
j)	0.47	0.47	0.71	0.77	0.94	0.59	0.94	1.06	0.47	0.55	0.81	0.77
k)	0.85	0.68	0.81	0.53	0.71	0.77	0.94	0.48	0.48	0.78	0.74	0.48
l)	0.90	0.57	0.68	0.73	0.98	0.72	0.87	0.64	0.54	0.72	0.83	0.59
m)	0.97	0.74	0.90	0.53	0.85	0.81	1.03	0.50	0.64	0.87	0.81	0.57
n)	0.92	0.57	0.70	0.73	0.98	0.72	0.87	0.68	0.59	0.73	0.83	0.64
o)	1.53	2.06	2.12	2.48+	2.24	1.98	1.53	2.48	1.71	1.90	2.06	2.10
p)	1.83	1.77	2.06	2.48	2.18	1.85	1.83	2.45	1.47	1.89	2.09	1.96
c/b	0.40	0.37	0.30	0.36+	0.37	0.37	0.37	-	0.30	0.36	0.37	-
c/e	0.70	0.60+	0.59+	0.64+	0.72	0.61	0.74	-	0.46+	0.63	0.68	-
d/e	1.19	1.13	1.07	1.12	1.09	1.08	1.15	-	1.11	1.13	1.11	-

Notes: Measurements are in mm, except for a), b), and c) which are in mm^2 and c/b and d/e which are dimensionless.

\+ = specimen slightly worn at the position of measurement, true value would be greater.

* = specimens heavily worn at the position of measurement, these values were excluded from text Figures, from regressions and from the calculation of mean values.

The bracketed value is greatly exaggerated by the cingulum and was excluded from text figures, from regressions and from calculations of mean values.

Gorilla gorilla: Enamel thickness sample data.

ID.	Tooth type	Sex	M-DC	B-LC	M-DCxB-IC	Museum no.
Go 1	Left M^1	M	14.6	16.1	235.1	M 1857.11.2.2
Go 2	Left M^2	M	16.2	17.3	280.3	M 1857.11.2.2
Go 3	Right M^3	M	17.3	16.4	283.7	M 1857.11.2.2
Go 4	Right M^1	M	15.5	16.1	249.6	M 1963.3.25.1
Go 5	Right M^2	M	15.6	16.8	262.1	M 1939.940
Go 6	Left M^3	M	14.6	15.8	230.7	M 1939.940
Go 7	Right M_1	M	16.2	13.6	220.3	M 1857.11.2.2
Go 8	Right M_2	M	18.8	14.7	276.4	M 1939.955
Go 9	Left M_3	M	18.1	14.8	267.9	M 1939.940
Go 10	Left M_1	M	16.3	14.4	234.7	M 1963.3.25.1
Go 11	Right M_2	M	18.2	15.5	282.1	M 1939.940
Go 12	Right M_3	M	>15.0	>12.6	-	M 1939.955
Go 13	Right M^1	F	14.8	15.2	225.0	M 1939.958
Go 14	Left M^2	F	14.1	15.1	212.9	M 1939.958
Go 15	Left M^3	F	15.1	14.9	225.0	M 1939.954
Go 16	Left M^1	F	14.9	15.5	231.0	M 1939.959
Go 17	Right M^2	F	14.9	15.8	235.4	M 1979.1322
Go 18	Right M^3	F	13.9	14.3	198.8	M 1979.1322
Go 19	Left M_1	F	16.4	13.5	221.4	M 1939.958
Go 20	Right M_2	F	16.3	14.6	238.0	M 1939.958
Go 21	Right M_3	F	18.3	14.7	269.0	M 1939.554
Go 22	Left M_1	F	>15.3	13.3	-	M 1979.1322
Go 23	Left M_2	F	16.5	14.6	219.5	M 1979.1322
Go 24	Left M_3	F	16.4	14.1	231.2	M 1979.1322

Notes: M-DC = mesial to distal crown length

B-LC = buccal to lingual crown breadth.

Enamel thickness measurements from buccal to lingual sections through the mesial cusps of Gorilla gorilla molars (see Figures 4.1 and 4.2 for explanation of the position and orientation of the measurements).

	G 1 M^1	G 13 M^1	G 16 M^1	G 2 M^2	G 5 M^2	G 17 M^2	G 6 M^3	G 15 M^3	G 18 M^3	M^1 Mean	M^2 Mean	M^3 Mean
a)	105.0+	91.2	107.5	136.6	124.0	96.9	110.2	100.0	80.5	101.2	119.2	96.9
b)	80.4	71.0	86.0	107.6	97.7	75.1	85.5	77.5	60.1	79.1	93.5	74.4
c)	24.6+	20.2	21.5	29.0	26.3	21.8	24.7	22.5	20.4	22.1	25.7	22.5
d)	29.9+	28.8	30.3	35.5	33.2	30.4	32.2	29.2	28.4	29.5	33.1	29.9
e)	27.2	26.8	27.8	31.3	31.8	26.9	28.4	27.0	24.3	27.3	30.0	26.6
f)	0.65	0.71	0.41	1.06	1.06	0.88	0.83	1.06	0.94	0.59	1.00	0.94
g)	0.65+	0.35	1.18	1.06	1.06	1.12	1.53	0.65	1.53	0.73	1.08	1.24
h)	0.88	0.77	0.68	0.99	1.06	0.77	0. 5	0.73	0.74	0.78	0.94	0.77
i)	0.83	0.71	1.06	0.79	0.86	0.61	1.06	0.88	0.59	0.87	0.75	0.84
j)	0.83	0.71	0.71	0.66	0.71	0.53	0.65	0.88	0.61	0.75	0.63	0.71
k)	0.94	0.88	0.77	1.05	0.90	1. 0	0.88	0.98	0.83	0.86	0.98	0.90
l)	1.00	0.73	0.83	0.99	0.78	0.92	1.06	1.05	1.10	0.85	0.90	1.07
m)	0.94	0.94	0.80	1.09	0.90	1.04	0.88	1.06	0.83	0.89	1.01	0.92
n)	1.06	0.74	0.94	1.06	0.85	1.00	1.12	1.24	1.12	0.91	0.97	1.14
o)	2.77	3.18	3.13	3.07	3.30	3.07	3.30	2.77	2.95	3.03	2.95	3.01
p)	2.77	3.48	2.36	3.07	3.30	2.83	2.59	3.18	2.36	2.87	2.87	2.71
c/b	0.31	0.28	0.25	0.27	0.27	0.29	0.29	0.29	0.34	0.28	0.27	0.31
c/e	0.90+	0.75	0.77	0.93	0.83	0.81	0.87	0.83	0.84	0.81	0.86	0.85
d/e	1.10	1.07	1.09	1.13	1.04	1.13	1.13	1.08	1.17	1.08	1.10	1.13

	G 7 M_1	G 10 M_1	G 8 M_2	G 11 M_2	G 20 M_2	G 23 M_2	G 9 M_3	G 21 M_3	G 24 M_3	M_1 Mean	M_2 Mean	M_3 Mean
a)	84.0	101.9+	114.4	103.7	96.0	91.2	86.7	87.8+	-	93.0	101.3	87.3
b)	63.5	84.4	82.1	76.5	70.5	71.6	61.5	65.1	63.9	74.0	75.2	63.5
c)	20.5	17.5+	32.3	27.2	25.5	19.6	25.2	22.7+	-	19.0	26.1	24.0
d)	25.8	30.1	31.4	29.9	30.3	30.0	27.2	26.3+	-	28.0	30.4	26.8
e)	23.0	28.2	28.4	26.9	26.5	26.8	23.9	24.5	24.4	25.6	27.2	24.3
f)	0.67	0.47*	0.83	0.59	0.94	0.59	1.18	1.30	-	0.57	0.74	1.24
g)	0.88	0.77	1.09	0.71	1.06	0.83	1.42	0.83	0.88	0.83	0.92	1.04
h)	0.94	0.83	1.30	1.06	0.88	0.64	1.00	1.27	-	0.89	0.97	1.14
i)	1.16	0.57	1.12	0.83	0.71	0.60	0.94	1.19	-	0.87	0.82	1.07
j)	1.14	0.65	1.42	1.06	0.71	0.67	1.77	1.30	-	0.90	0.97	1.54
k)	0.85	0.83	1.24	1.32	0.93	0.94	1.36	0.93	0.94	0.84	1.11	1.08
l)	1.04	0.83	0.88	1.01	0.91	0.83	1.12	0.80	0.91	0.94	0.91	0.94
m)	0.88	0.88	1.30	1.53	1.01	1.03	1.53	1.04	1.06	0.88	1.22	1.21
n)	1.30	0.83	0.94	1.03	0.94	0.83	1.16	0.92	1.00	1.07	0.94	1.03
o)	2.12	2.95	3.54	3.42	3.07	3.77	2.95	2.59	2.24	2.54	3.45	2.59
p)	1.91	2.65	3.28	3.30	2.95	3.54	2.71	3.07	3.66	2.28	3.27	3.15
c/b	0.32	0.21+	0.39	0.36	0.36	0.27	0.41	0.35+	-	0.27	0.35	0.38
c/e	0.89	0.62+	1.14	1.01	0.96	0.73	1.05	0.93+	-	0.76	0.96	0.99
d/e	1.12	1.07	1.11	1.11	1.14	1.12	1.14	1.07+	-	1.10	1.12	1.11

Notes: Measurements are in mm, except for a), b) and c) which are in mm^2, and c/b and d/e which are dimensionless.

\+ = specimen slightly worn at the position of measurement, true value would be greater.

* = specimen heavily worn at the position of measurement, these values were excluded from text Figures, from regressions and from the calculation of mean values.

Homo sapiens: Enamel thickness sample data.

ID.	Tooth type	Sex	M-DC	B-LC	M-DCxB-LC	Museum no.
Ho 1	Left M^1	?	9.4	10.9	102.5	M 4.5431
Ho 2	Left M^2	?	8.7	10.7	93.1	M 4.5431
Ho 3	Left M^3	?	8.7	11.0	95.7	M 4.5440
Ho 4	Left M^1	?	9.9	11.5	113.9	M 4.5434
Ho 5	Left M^2	?	[illegible]	10.9	[illegible]	M 4.5381
Ho 6	Left M^3	?	8.9	11.1	98.8	M 4.5381
Ho 7	Right M_1	?	10.5	9.9	104.0	M 4.5345
Ho 8	Right M_2	?	11.7	10.1	118.2	M 4.5226
Ho 9	Left M_3	?	10.8	9.9	106.9	M 4.5383
Ho 10	Right M_1	?	9.8	9.6	94.1	M 4.5265
Ho 11	Right M_2	?	10.4	9.6	99.8	M 4.5265
Ho 12	Left M_3	?	10.8	9.7	104.8	M 4.5269
Ho 13	Right M^1	?	10.7	11.8	126.3	M 4.5430
Ho 14	Right M^2	?	10.2	12.5	127.5	M 4.5430
Ho 15	Left M^3	?	8.9	11.7	104.1	M 4.5434
Ho 16	Left M^1	?	-	10.9	-	M 4.5440
Ho 17	Left M^2	?	8.6	10.9	93.7	M 4.5440
Ho 18	Left M^3	?	9.9	12.6	124.7	M 4.5448
Ho 19	Right M_1	?	11.0	10.9	119.9	M 4.5226
Ho 20	Left M_2	?	10.3	9.7	99.9	M 4.5224
Ho 21	Right M_3	?	9.5	9.0	85.5	M 4.5224
Ho 22	Right M_1	?	10.3	9.6	98.9	M 4.5217
Ho 23	Right M_2	?	9.9	9.1	90.1	M 4.5217
Ho 24	Right M_3	?	11.4	9.7	110.6	M 4.5217

Notes: M-DC = mesial to distal crown length

B-LC = buccal to lingual crown bre dth.

Enamel thickness measurements from buccal to lingual s ctions through the mesial cusps of Homo sapiens molars (see Figures 4.1 and 4.2 for explanation of the position and orientation of the measurements).

	Ho 1 M^1	Ho 13 M^1	Ho 16 M^1	Ho 14 M^2	Ho 17 M^2	Ho 3 M^3	Ho 6 M^3	Ho 18 M^3	M^1 Mean	M^2 Mean	M^3 Mean
a)	46.7*	69.5	48.9	71.3	50.7+	59.4	53.4	68.4	55.0	61.0	60.4
b)	34.2	41.0	31.5	37.0	35.5	39.2	36.6	45.6	35.6	36.3	40.5
c)	12.5*	28.5	17.4	34.3	15.2+	20.2	16.8	22.8	19.5	24.8	19.9
d)	19.8+	24.0	21.9	24.4	20.9	23.1	21.3	25.2	21.9	22.7	23.2
e)	18.7	19.6	17.7	19.1	18.6	18.1	16.7	19.8	18.7	18.9	18.2
f)	-	1.18	1.00	1.65	0.94	1.36	1.36	1.42	1.09	1.30	1.38
g)	-	2.00	0.59	2.06	1.06	1.42	1.30	1.42	1.30	1.56	1.38
h)	0.59*	1.26	0.92	1.89	1.12	1.18	0.88	1.10	1.09	1.51	1.05
i)	0.71*	1.39	0.92	2.06	1.06	1.06	0.87	1.24	1.01	1.56	1.06
j)	0.68	1.53	0.59	1.77	1.06	1.36	1.06	1.53	0.93	1.42	1.32
k)	1.09	1.44	1.05	1.38	0.84	1.04	0.94	0.92	1.19	1.11	0.97
l)	0.93	1.85	1.16	2.24	0.91	1.18	1.37	1.38	1.31	1.58	1.31
m)	1.09	1.45	1.06	1.42	0.86	1.04	0.98	0.92	1.20	1.14	0.98
n)	0.98	1.89	1.24	2.44	0.97	1.24	1.46	1.44	1.37	1.71	1.38
o)	-	2.48	1.83	2.36	2.24	1.71	1.06	1.77	2.16	2.30	1.51
p)	-	1.65	2.24	1.95	2.12	1.65	1.18	1.77	1.95	2.24	1.53
c/b	0.37*	0.70	0.55	0.93	0.43+	0.52	0.46	0.50	0.63	0.68	0.49
c/e	0.67*	1.45	0.98	1.80	0.82+	1.12	1.01	1.15	1.22	1.31	1.09
d/e	1.06*	1.22	1.24	1.28	1.12	1.28	1.28	1.27	1.23	1.20	1.27

	Ho 10 M_1	Ho 19 M_1	Ho 22 M_1	Ho 8 M_2	Ho 23 M_2	Ho 12 M_3	Ho 24 M_3	M_1 Mean	M_2 Mean	M_3 Mean
a)	53.7	51.8+	42.6	50.4	36.7	51.8	45.4	47.2	43.6	48.6
b)	28.6	37.3	28.1	27.0	18.8	31.9	25.8	32.7	22.9	28.9
c)	25.1	14.5*	14.5	23.4	17.9	19.9	19.6	14.5	20.7	19.8
d)	20.5	20.4	19.0	21.2	17.6	21.6	20.3	19.7	19.4	21.0
e)	15.4	18.5	15.7	15.9	12.8	16.4	15.1	17.1	14.4	15.8
f)	1.67	0.94	0.77	1.77	1.12	1.42	1.36	0.86	1.45	1.39
g)	2.18	1.00	1.00	1.53	1.36	1.39	1.18	1.00	1.45	1.29
h)	1.73	1.04	1.06	1.41	0.94	1.27	1.24	1.05	1.18	1.26
i)	1.79	0.94	1.01	1.27	0.93	1.09	1.27	0.98	1.10	1.18
j)	1.91	1.06	0.59	1.18	0.59	1.44	1.18	0.83	0.89	1.31
k)	1.14	1.58	1.18	1.79	1.53	0.94	1.16	1.38	1.66	1.05
l)	1.51	0.94	1.14	1.10	1.16	1.16	1.18	1.04	1.13	1.17
m)	1.14	1.70	1.39	1.86	1.56	0.94	1.26	1.55	1.71	1.10
n)	1.58	0.97	1.14	1.10	1.16	1.18	1.24	1.06	1.13	1.21
o)	1.51	1.77	1.47	1.77	1.42	1.30	1.59	1.62	1.60	1.45
p)	1.04	1.71	1.24	2.01	1.18	1.92	1.77	1.48	1.60	1.85
c/b	0.88	0.39+	0.52	0.87	0.95	0.62	0.76	0.46	0.91	0.69
c/e	1.63	0.78*	0.92	1.47	1.40	1.21	1.30	0.85	1.44	1.26
d/e	1.33	1.10	1.21	1.33	1.38	1.32	1.34	1.16	1.36	1.33

Notes: Measurements are in mm, except for a), b) and c) which are in mm^2, and c/b and d/e which are dimensionless.

+ = specimen slightly worn at the position of measurement, true value would be greater.

* = specimen heavily worn at the position of measurement, these values were excluded from text Figures, from regressions and from the calculation of mean values.

Pongo pygmaeus: Enamel thickness sample data.

ID.	Tooth type	Sex	M-DC	B-LC	M-DCxB-LC	Museum no.
Po 1	Left M^1	M	13.1	13.2	172.9	M 1976.1439
Po 2	Left M^2	M	13.2	14.4	190.1	M 1976.1439
Po 3	Left M^3	M	12.4	13.1	162.4	M 1976.1439
Po 4	Left M^1	M	11.9	13.3	158.3	M 1976.1435
Po 5	Left M^2	M	12.2	13.9	169.6	M 1976.1435
Po 6	Left M^3	M	12.7	14.1	179.1	M 1976.1435
Po 7	Left M_1	M	12.9	11.5	148.4	M 1976.1414
Po 8	Left M_2	M	14.8	12.7	188.0	M 1976.1435
Po 9	Right M_3	M	15.6	13.5	210.6	M 1976.1435.
Po 10	Right M_1	M	13.0	12.3	159.9	M 1976.1439
Po 11	Right M_2	M	14.1	13.4	188.9	M 1976.1439
Po 12	Right M_3	M	13.3	>11.9	-	M 1976.1439
Po 13	Right M^1	F	12.8	13.1	167.7	M 1976.1444
Po 14	Right M^2	F	11.7	13.5	158.0	M 1976.1444
Po 15	Left M^3	F	12.1	13.3	160.9	M 1976.1444
Po 16	Right M^1	F	11.5	12.9	148.4	M 1976.1441
Po 17	Right M^2	F	11.2	13.1	146.7	M 1976.1441
Po 18	Left M^3	F	11.7	13.8	161.5	M 1976.1415
Po 19	Left M_1	?	13.5	12.3	166.1	M 1976.1410
Po 20	Left M_2	F	13.6	12.7	172.7	M 1976.1441
Po 21	Left M_3	F	13.1	11.1	145.4	M 1976.1441
Po 22	Left M_1	F	14.0	11.8	165.2	M 1976.1444
Po 23	Right M_2	F	14.2	13.2	1 7.4	M 1976.1444
Po 24	Right M_3	F	14.8	12.9	190.9	M 1976.1444

Notes: M-DC - mesial to di t l crown l n th

B-LC buccal to ling al crown breadth.

Enamel thickness measurements from buccal to lingual sections through the mesial cusps of Pongo pygmaeus molars (see Figures 4.1 and 4.2 for explanation of the position and orientation of the measurements).

	Po 1 M^1	Po 13 M^1	Po 16 M^1	Po 5 M^2	Po 14 M^2	Po 17 M^2	Po 3 M^3	Po 15 M^3	Po 18 M^3	M^1 Mean	M^2 Mean	M^3 Mean
a)	70.9	70.6	64.4	72.0	77.8	70.4	-	71.1	65.0	68.6	73.4	68.1
b)	53.7	49.0	43.9	48.8	52.6	49.2	-	45.6	41.7	48.9	50.2	43.7
c)	17.2	21.6	20.5+	23.2	25.2	21.2	-	25.5	23.3	19.8	23.2	23.9
d)	23.1	23.8	22.7	24.1	25.3	24.7	-	24.3	23.4	23.2	24.7	23.9
e)	20.8	20.6	20.1	20.5	21.2	19.9	-	19.7	19.6	20.5	20.5	19.7
f)	0.85	1.00	0.92	0.94	1.12	1.00	1.12	1.42	1.18	0.92	1.02	1.24
g)	0.71	0.94	0.65*	1.24	1.36	1.30	1.18	1.77	1.42	0.83	1.30	1.46
h)	0.86	1.04	0.99	1.22	1.22	1.06	1.04	1.53	1.05	0.96	1.17	1.21
i)	0.98	1.04	1.12	1.11	1.29	1.17	1.16	1.42	1.25	1.05	1.19	1.28
j)	0.88	0.94	1.00	1.30	1.18	0.77*	0.83	1.06	1.42	0.94	1.24	1.10
k)	1.01	1.18	1.03	1.04	1.05	1.06	1.26	1.25	1.06	1.07	1.05	1.19
l)	1.17	1.44	1.33	1.23	1.57	1.29	1.30	1.32	1.22	1.31	1.36	1.28
m)	1.09	1.19	1.06	1.06	1.06	1.11	1.27	1.25	1.10	1.11	1.08	1.21
n)	1.30	1.57	1.42	1.38	1.63	1.34	1.36	1.46	1.53	1.43	1.45	1.45
o)	1.39	1.36	1.50	1.89	1.47	1.42	1.00	1.42	1.77	1.42	1.59	1.40
p)	1.53	1.42	1.36	1.59	1.24	1.18	0.94	1.06	1.53	1.44	1.34	1.18
c/b	0.32	0.44	0.47+	0.48	0.48	0.43	-	0.56	0.56	0.41	0.46	0.55
c/e	0.83	1.05	1.02+	1.13	1.19	1.07	-	1.29	1.19	0.97	1.13	1.22
d/e	1.11	1.16	1.13	1.18	1.19	1.24	-	1.23	1.19	1.13	1.20	1.21

	Po 10 M_1	Po 19 M_1	Po 22 M_1	Po 8 M_2	Po 11 M_2	Po 20 M_2	Po 9 M_3	Po 21 M_3	Po 24 M_3	M_1 Mean	M_2 Mean	M_3 Mean
a)	59.4	64.9	71.2	62.1	62.0	65.6+	64.8	54.3	69.3	65.2	63.2	62.8
b)	42.0	46.0	52.2	41.5	41.8	45.5	45.5	34.5	44.2	46.7	42.9	41.4
c)	17.4+	18.9	19.0+	20.6+	20.2+	20.1+	19.3	19.8	25.1	19.1	20.3	21.4
d)	20.8	22.2	23.8	21.9	21.6	23.9	23.3	21.4	24.3	22.3	22.5	23.0
e)	18.5	20.4	21.4	19.1	18.7	20.1	19.7	16.9	18.5	20.1	19.3	18.4
f)	0.77	1.06	0.35*	0.71*	1.06	1.00	1.42	1.42	1.59	0.92	1.03	1.48
g)	0.83	1.02	0.59*	1.12	1.36	1.18	1.18	1.42	1.53	0.93	1.22	1.38
h)	1.14	1.46	1.04	1.42	1.42	1.34	1.18	1.30	1.42	1.21	1.39	1.30
i)	1.10	1.39	0.74	0.91	1.18	1.18	1.18	1.30	1.30	1.08	1.09	1.26
j)	1.12	1.47	0.83	1.30	1.24	1.30	1.18	1.36	1.20	1.14	1.28	1.25
k)	1.18	1.16	1.05	0.87	1.18	0.97	1.06	1.07	1.32	1.13	1.01	1.15
l)	0.96	0.92	1.12	1.09	1.09	0.94	1.13	1.07	1.26	1.00	1.04	1.15
m)	1.53	1.42	1.44	0.98	1.43	1.07	1.07	1.22	1.57	1.46	1.16	1.29
n)	0.97	0.92	1.14	1.12	1.11	0.94	1.13	1.07	1.34	1.01	1.06	1.18
o)	1.59	2.18	2.01	2.12	1.89	1.95	1.65	1.36	1.12	1.93	1.99	1.38
p)	1.53	2.24	1.77	1.71	1.59	1.77	1.89	1.36	1.18	1.85	1.69	1.48
c/b	0.41+	0.41	0.36+	0.50+	0.48+	0.44+	0.42	0.57	0.57	0.41	0.47	0.52
c/e	0.94+	0.93	0.89+	1.08+	1.08+	1.00+	0.98	1.17	1.36	0.95	1.05	1.17
d/e	1.12	1.09	1.11	1.15	1.16	1.19	1.18	1.27	1.31	1.11	1.17	1.25

Notes: Measurements are in mm, except for a), b) and c) which are in mm^2, and c/b and d/e which are dimensionless.

\+ = specimens slightly worn at the position of measurement, true value would be greater.

* = specimens heavily worn at the position of measurement, these values were excluded from text Figures, from regressions and from the calculation of mean values.

Later Miocene hominoids: Enamel thickness sample data.

Taxon	Mus.No.	Tooth type	M-DC	B-LC	M-DCxB-LC
S.sivalensis	M 13365	Right M^1	11.6	12.7	147.3
S.sivalensis	M 13366	Right M^1	11.6	13.2	153.1
S.punjabicus	M 13367	Left M_3	14.0	11.4	159.6
S.darwini	BP 4	Right M_3	14.7	13.0	191.1
S.darwini	BP 37	Right M^2	11.1	13.2	146.5
S.darwini	BP 64	Left M_2	13.9	12.3	171.0
S.alpani	BP 12	Right M_3	12.3	9.8	120.5
S.alpani	BP 13	Right M_2	11.4	10.5	119.7
S.alpani	BP 14	Left M_1	9.8	8.7	85.3
.alpani	BP 17	Left M_2	11.1	9.8	108.8
S.alpani	BP 29	Right M^2	11.3	12.8	144.6

Notes: M-DC = mesial to distal crown length

B-LC = buccal to lingual crown breadth.

Enamel thickness measurements from buccal to lingual sections through the mesial cusps of Sivapithecus molars (see Figures 4.1 and 4.2 for explanation of the position and orientation of the measurements).

	BP 4 M_3	BP 12 M_3	BP 13 M_2	BP 14 M_1	BP 17 M_2	BP 29 M^2	BP 37 M^2	BP64 M_2	M 13365 M^1	M 13366 M^1	M 13367 M_3
a)	75.1	-	49.7	36.8	46.0	58.8	56.0	64.5	50.8	52.3	56.7
b)	46.1	-	32.4	25.7	29.4	35.3	35.8	44.4	34.1	32.2	34.4
c)	29.0	-	17.3	11.1++	16.6	23.5	20.2	20.1+	16.7+	20.1+	22.3+
d)	23.8	-	19.7	16.8	18.3	21.9	20.8	22.1	20.4	20.0	21.1
e)	18.8	-	16.3	14.8	15.7	17.7	17.8	18.7	17.7	17.3	16.8
f)	1.89	1.89	1.18	0.53++	1.47	1.42+	0.98	0.71++	0.94	0.94	1.53
g)	1.53	1.42	1.00	0.74++	1.10	2.12	0.94	1.00++	1.18	0.83+	1.65
h)	1.73	1.39	1.10	1.00	1.57	1.34	0.98	1.20	1.06	1.10	1.32
i)	1.65	1.36	1.12	1.06	1.42	1.53	1.19	1.30	1.06	1.20	1.63
j)	1.53	1.42	0.94	1.12	1.59	1.42	1.00	1.30	0.94	1.30	1.18
k)	2.09	1.30	1.26	1.19	1.16	0.59	1.20	1.30	0.76	1.17	0.79
l)	1.42	0.71	0.94	0.61	0.81	1.19	1.66	1.23	1.36	1.56	1.00
m)	2.83	1.79	1.73	1.40	1.59	0.61	1.30	1.47	0.81	1.19	0.92
n)	1.42	0.71	0.96	0.61	0.83	1.34	1.89	1.27	1.51	1.91	1.03
o)	0.71	0.59	1.30	1.24	1.06	1.89	1.62	1.42	1.89	1.53	1.65
p)	1.06	1.65	1.36	1.24	1.44	1.42	1.47	1.59	1.42	1.53	1.42
c/b	0.63	-	0.53	0.43++	0.56	0.67	0.56	0.45+	0.49+	0.62+	0.65+
c/e	1.54	-	1.06	0.75++	1.06	1.33	1.13	1.07+	0.94+	1.16+	1.33+
d/e	1.27	-	1.21	1.14	1.17	1.24	1.17	1.18	1.15	1.16	1.26

Notes: Measurements are in mm, except for a), b) and c) which are in mm^2 and c/b and d/e which are dimensionless.

\+ = specimen slightly worn at the position of measurement, true value would be greater.

++ = specimen heavily worn at the position of measurement, true value would be considerably greater.